UNIVERSITE DU QUEBEC A MONTREAL

# ACCLIMATATION NUTRITIVE ET RÉGÉNÉRATION DE L'ÉRABLE À SUCRE SELON L'ENRICHISSEMENT EN ESPÈCES CONIFÉRIENNES

THESE

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# AVANT-PROPOS

Cette thèse est rédigée sous forme d'articles. Une introduction générale reprenant les bases de la littérature sur le sujet est ainsi suivie de trois chapitres sous la forme d'articles scientifiques rédigés en anglais. Les articles sont publiés dans des revues avec comité de lecture (Chapitre I et III), ou en préparation pour soumission (Chapitre II). Pour cette raison, la forme peut changer de l'un à l'autre. Des répétitions entre les chapitres sont également inévitables. Afin d'alléger l'ensemble du manuscrit, les références bibliographiques de chaque chapitre ont été compilées à la fin du document. Je suis le premier auteur de chacun des chapitres de cette thèse, ayant réalisé l'ensemble du travail depuis la collecte des données jusqu'à la rédaction. Mon directeur Nicolas Bélanger ainsi que mon codirecteur Christian Messier ont suivi chaque étape de cette thèse et ont contribué à la rédaction des chapitres. Steven W. Kembel et Benoit Côté ont fait partit du comité de projet de cette thèse et ont respectivement contribués à l'amélioration du chapitre II et III. Mario Fontana a contribué à l'élaboration des balances nutritives foliaires et à l'amélioration du chapitre III.

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# RÉSUMÉ

Durant les dernières décennies, de nombreuses modifications de la distribution des espèces forestières se sont effectuées à leur marge de distribution et dans la direction prédite par les modèles tenant compte des changements climatiques. Cependant, ces modifications se sont effectuées à une intensité moindre que celle initialement prédite sur la seule base des enveloppes climatiques. De récentes évidences suggèrent que d'importants facteurs non climatiques (e.g. interactions plante-sol, plante-plante et plante-insecte) au sein des milieux résidents sont responsables de cette différence, en compliquant l'établissement, la croissance et la survie des espèces migrantes. L'érable à sucre (*Acer saccharum* Marsh.) représente une espèce d'étude de choix considérant son importance écologique et économique dans l'Est de l'Amérique du Nord ainsi que son actuelle situation migratoire. Des études récentes suggèrent que son exigence nutritionnelle limiterait l'établissement de ses semis au sein de la forêt boréale, dont les sols dominés par les conifères sont classiquement très acides et pauvres en éléments nutritifs. D'autre part, plus au Sud de sa distribution, son remplacement progressif par le hêtre (*Fagus grandifolia* Erhr) suggère qu'il risque de subir une contraction de sa distribution. Le but général de cette thèse de doctorat a été d'étudier un élément important permettant de mieux prédire la migration de l'érable à sucre, soit l'acclimatation nutritive et la régénération de ses semis aux conditions de sol et de couvert aux limites de sa distribution. L'hypothèse a été émise d'une part que la présence de conifères engendre un débalancement nutritionnel foliaire chez les semis d'érable à sucre pouvant mener à un échec de régénération, et d'autre part que la présence de hêtre peut empêcher la régénération de l'érable à sucre au travers d'une canopée plus dense.

Dans le premier chapitre, l'évolution des concentrations nutritives foliaires de semis d'érable à sucre a été étudiée le long d'un gradient d'enrichissement en espèces résineuses et sur 3 sites représentant le maximum de distribution latitudinal de l'érable à sucre au Québec. Les résultats de ce chapitre ont démontré que les espèces conifériennes ont un effet négatif sur la nutrition foliaire des semis d'érable à sucre parce qu'ils réduisent le Ca et Mg foliaire, lesquels sont reconnus comme importants pour leur croissance et survie. Cet effet a été observé indépendamment de la localisation étudiée, et résulte d'une plus forte acidité du sol conditionnée par la

présence des conifères. Les semis poussant le plus au Nord avaient également des concentrations nutritives foliaires plus faibles, ce qui peut donc exacerber l'effet négatif de la présence des conifères. Dans le deuxième chapitre, l'emphase a été mise sur les facteurs affectant les échecs de régénération de l'érable à sucre au sein de sa distribution au Québec. D'une part, les résultats indiquent que la régénération de l'érable à sucre au sein de forêts de conifères pourrait être dépendante du type de conifères présents et lié aux caractéristiques du sol. La probabilité d'établissement de l'érable à sucre serait très faible, voire improbable, sur des sites au sol très acide dominés par la pruche ou encore le cèdre. Cependant, dans d'autres cas et sous des conditions très spécifiques, la dissolution des minéraux serait favorisée en présence de certains conifères tels que l'épicéa, le sapin ou encore le pin, ce qui peut faciliter la nutrition des semis d'érable à sucre. D'autre part, les résultats indiquent que la présence de hêtre peut empêcher la régénération des semis d'érable à sucre via une canopée plus dense qui provoque une plus faible disponibilité de la lumière à un seuil critique pour leur survie. Enfin, le troisième chapitre aborde la nutrition foliaire des semis d'érable à sucre sous couvert résineux en utilisant le concept des balances nutritives foliaires. Cette méthode novatrice a été également testée dans un but comparatif sur l'érable rouge dont la distribution s'est étendue avec un meilleur succès que celle de l'érable à sucre au cours du dernier siècle. Les résultats ont permis de confirmer que la présence de conifères entraîne un débalancement nutritif des semis d'érable à sucre, dans le même sens que celui des arbres matures diagnostiqués en déclin suite à l'appauvrissement en Ca et Mg dans les sols forestiers par les retombées acides. D'autre part, les résultats ont permis d'identifier que l'érable rouge est capable de maintenir un équilibre nutritionnel foliaire avec l'augmentation de l'abondance en conifères. Cette observation est le résultat d'une plus grande plasticité nutritionnelle face à des conditions environnementales contrastées et probablement la cause des différences de succès migratoire observées entre ces deux espèces.

En conclusion, il apparait que les conditions de sol au sein de la forêt boréale sont très probablement une des raisons ralentissant la migration de l'érable à sucre. Afin de favoriser sa migration au sein de la forêt boréale, une expansion assistée de sa distribution pourrait être effectuée juste après sa limite de distribution sur les sols considérés comme les plus propices et couplé à des méthodes de chaulage. Dans un autre contexte, une suppression des gaulis de hêtre avec une récolte de faible intensité des hêtres matures permettrait de limiter le remplacement de l'érable à sucre par le hêtre au sein des peuplements à forte valeur socio-économique. De manière générale, les résultats de cette thèse soulignent l'importance des interactions biotiques comme facteurs clés influençant la limite de distribution des espèces végétales en général.

*Mots-clés* : Érable à sucre, nutrition foliaire, régénération, semis, acidité du sol, conifères, hêtre.

# INTRODUCTION

L'écosystème forestier représente 30% des surfaces terrestres, contient deux tiers de la diversité mondiale des espèces terrestres et stocke 45% du carbone terrestre de la planète (Bonan 2008). A l'échelle continentale, la composition et la distribution des espèces végétales au sein de cet écosystème sont principalement déterminées par le climat (Woodward 1987, Neilson 1995). Cependant, au cours du dernier siècle, celui-ci a subi un réchauffement global dû à la hausse des émissions anthropogéniques de gaz à effet de serre, tel que le dioxyde de carbone ($CO_2$). La température a ainsi augmenté d'environ 0,85°C depuis la fin du 19$^{ème}$ siècle et devrait continuer d'augmenter d'environ 2 à 4°C jusqu'à la fin du siècle (Collins et al. 2013, Hartmann et al. 2013). Les modèles de prévision suggèrent également que la disponibilité en eau et la sévérité des sécheresses devraient respectivement diminuer et augmenter au cours de l'été dans les régions centrales et de l'est du Canada (Dai 2011, Van Oldenborgh et al. 2013). La croissance et la distribution des espèces végétales au sein de l'écosystème forestier étant fortement influencés par les régimes hydriques (Neilson et al. 2005, McKenney et al. 2007, Brassard et al. 2009), il est donc attendu que ces changements climatiques créent des contraintes physiologiques forçant les plantes à trouver de nouveaux optimum écologiques en déplaçant leur distribution à des latitudes et altitudes plus élevées. Bien que les espèces végétales aient répondu aux changements climatiques tout au long de leur histoire évolutive, la principale préoccupation qui distingue les changements actuels de ceux du passé est la vitesse à laquelle ils se produisent (Root et al. 2003). Le sort des écosystèmes forestiers face aux changements climatiques est particulièrement important pour le Québec en raison de leur importance économique et écologique.

De nombreuses synthèses suggèrent que des changements de la distribution des plantes, favorisés par une modification de leur physiologie, phénologie et croissance en réponse à l'augmentation des températures moyennes annuelles, se sont déjà produits au cours des 30 à 40 dernières années (e.g. Rosenzweig et al. 2008, Chen et al. 2011). Récemment, une emphase a été mise sur l'importance des zones de transition végétales (altitudinale et latitudinales) pour observer les réponses des espèces aux changements climatiques (Beckage et al. 2008, Fisichelli et al. 2014). Les espèces qui se développent au sein des limites de transition végétales sont généralement proches de leurs limites écophysiologiques. De petits changements dans les conditions environnementales au sein de ces zones peuvent ainsi causer des déplacements observables de la distribution des espèces végétales (Parmesan 2006). Par exemple, en Europe, il a été observé une élévation en altitude d'environ 29 m par décennie de l'optimum spécifique chez 170 espèces de plantes forestières depuis 1905 (Lenoir et al. 2008).

Afin de comprendre et prédire la migration des espèces végétales sous ces changements climatiques, de nombreuses études se sont basés sur des enveloppes environnementales et la corrélation avec la distribution actuelle des espèces (Guisan and Thuiller 2005). Certaines ont ainsi prédit un déplacement latitudinal et altitudinal de la distribution des espèces suivant les scénarios de changements climatiques. Par exemple, Iverson et al (2008) ont simulés les déplacements de distribution de 134 espèces d'arbres de l'Est de l'Amérique du Nord. Sous le scénario de changements actuels, environ 50% des espèces faisaient des gains alors que 40% des espèces faisaient des pertes d'habitat. Cependant, Zhu et al. (2012) ont récemment comparé les latitudes actuelles de semis et d'arbres matures respectifs de l'Est des U.S.A. avec leurs limites de distribution (selon l'inventaire du service forestier USDA) et sont venus à la conclusion que ces espèces s'adapteraient mal aux changements climatiques étant donné que 58,7% des espèces montrent des patterns caractéristiques d'une contraction de distribution. Bien que l'emphase de la recherche soit

actuellement mise sur un effet majeur du climat, ces résultats mettent en évidence le manque de preuve pour une réponse généralisée de la redistribution des habitats des espèces seulement contrôlée par le climat. Des évidences récentes démontrent au contraire que d'importants facteurs autre que le climat doivent être considérés pour améliorer notre capacité à prédire les déplacements des espèces suivant les changements climatiques (McMahon et al. 2011, Fisichelli et al. 2013, Brown and Vellend 2014, Graignic et al. 2014, Zhang et al. 2015). Par conséquent, il y a actuellement un besoin d'étudier les contraintes physiologiques des différentes espèces végétales conjointement avec leur capacité de dispersion et de germination afin de mieux prédire leur évolution dans le futur.

En outre, il reste encore beaucoup d'incertitudes quant à la façon dont les changements climatiques vont influencer l'établissement et la performance des semis durant les premières années suivant la germination. L'établissement, la croissance et la survie des semis sont des phases critiques pour le développement et la stabilité des espèces végétales (Walck et al. 2011). Ainsi, de petites différences de performance peuvent être suffisantes pour basculer le patron de compétitivité en faveur d'une autre espèce mieux adaptée aux conditions locales de l'environnement. Du fait de leur système racinaire encore peu développé et de leurs petites réserves nutritives, les semis sont beaucoup moins tolérants aux modifications des conditions climatiques et pédologiques que les individus adultes (Jackson et al. 2009). Par exemple, les semis sont généralement plus sensibles aux extrêmes de température et à la sécheresse que les plantes adultes car leur système racinaire de surface ne permet l'accès qu'à une partie des ressources en eau du sol (Niinemets 2010, Wright et al. 2013). D'autre part, certaines études sur les patrons et les performances des gaulis et des arbres à l'échelle du paysage suggèrent que l'intensité et même la direction de la réponse aux variables climatiques et environnementales peuvent changer avec l'ontogénie. Par exemple, Fisichelli et al. (2014) ont observés des réponses contraires de croissance et de survie

entre semis et gaulis d'une même espèce face à une augmentation de la température, ces contrastes étant reliés à des changements de tolérance et de stratégie afin de pallier aux fluctuations de la disponibilité en eau et de la température de saison de croissance. De telles différences de réponse avec l'ontogénie pourraient expliquer pourquoi certaines études (Zhu et al. 2012) n'ont pas observés de migration pour certaines espèces en réponse aux changements climatiques.

## 0.1 Contraintes locales à l'établissement des espèces

Sous les changements climatiques, les arbres doivent rapidement disperser leurs graines sur de longues distances et s'adapter aux conditions du milieu résident (autres que le climat) afin de coloniser assez rapidement de façon à compenser leur perte d'habitat. Les taux de dispersion des graines sont connus pour la plupart des espèces forestières canadiennes (Clark et al. 1998). Cependant, il reste encore beaucoup d'incertitude sur la façon dont les arbres s'adaptent aux nouveaux environnements. Lorsque les glaciers ont reculé, les espèces végétales ont migré vers le Nord dans des environnements encore primitifs et en pleine organisation (Jackson and Overpeck 2000). Au cours des siècles, les environnements résidents se sont développés en systèmes complexes propres aux espèces locales et qui peuvent constituer des contraintes aux espèces migrantes (i.e. au travers d'interactions biotiques et des propriétés de l'environnement). Ainsi, la réponse des plantes au climat devrait varier selon leur adaptation locale (Reich and Oleksyn 2008), les contraintes physiologiques spécifiques à l'espèce et le stade de vie étudié (émergence, développement et survie, croissance) (Fisichelli et al. 2014).

La régénération des arbres est contrôlée par de nombreuses variables biotiques et abiotiques qui sont inter-reliées et corrélées (Grubb 1977, Arii and Lechowicz 2002, McEwan et al. 2011). Ces variables peuvent être groupées en plusieurs ensembles conducteurs tels que le climat, la composition de la végétation dominante,

l'environnement ainsi que la végétation du sous-bois qui, de par leurs interrelations et leur chevauchement, ont différents degrés d'influence sur la régénération des arbres (Fisichelli et al. 2013). Par exemple, la composition des arbres dominants, qui est elle-même en partie le résultat du climat (Barnes et al. 1998), affecte fortement les processus et propriétés de l'environnement du sous-bois tel que la disponibilité en nutriments, les conditions de germination et la lumière disponible (Frelich et al. 1993, Finzi et al. 1998). L'environnement du sous-bois, incluant la texture et le pH du sol, ainsi que la disponibilité en lumière ne contrôle pas seulement la régénération des arbres mais également la composition de la végétation compétitrice du sous-bois (Canham et al. 1996, Walters and Reich 1996). Les conditions environnementales telles que la texture du sol sont également partiellement déterminées par le climat (Henne et al. 2007). La végétation du sous-bois ainsi que les herbivores spécialisés vont agir comme des filtres qui détermineront qu'elles espèces d'arbre seront capables de survivre et de dominer avec succès l'étage de régénération (Côté et al. 2004, Royo and Carson 2006).

Au sein des communautés végétales, le concept d'action rétroactive sur l'environnement (« positive feedbacks », Wilson and Agnew 1992)) implique que certaines espèces se sont créées des conditions bénéfiques dans l'environnement résident (pH et nutriments disponibles dans le sol, disponibilité en eau et lumière, présence de substances allélopathiques, régime de feu, etc...). Cependant, ces conditions compliquent l'établissement, la nutrition, la croissance et la survie des espèces migrantes. La présence d'herbivores et de pathogènes, ou encore l'absence d'organismes facilitateurs peuvent aussi diminuer le succès de la colonisation de l'espace résident (Guisan and Thuiller 2005). Par conséquent, il est crucial de bien comprendre l'effet des sols résidents (Lafleur et al. 2010) et des espèces résidentes (Ettinger and HilleRisLambers 2013) sur les espèces migrantes pour pouvoir prédire la redistribution des espèces suivant les changements climatiques.

## 0.2 Le cas de l'érable à sucre

La transition entre la forêt tempérée et la forêt boréale de l'Est de l'Amérique du Nord est un endroit idéal pour détecter les réponses des espèces aux changements climatiques (Goldblum and Rigg 2010). L'érable à sucre (*Acer saccharum*, Marsh. – noté ES par la suite), en particulier, représente une espèce d'étude de choix étant donné son importance écologique et économique dans l'Est de l'Amérique du Nord, la quantité de données disponibles sur cette espèce ainsi que son actuelle situation migratoire. L'ES et le sapin baumier (*Abies balsamea*, AB) coexistent à la transition entre la forêt tempérée et la forêt boréale. La présence d'îlots retranchés d'ES au-delà de sa distribution nordique suggère que cette espèce n'est pas directement limitée par le climat (Graignic et al. 2014). Cependant, le fait que l'ES ne soit pas une espèce dominante au sein de la forêt boréale démontre que le climat à, au final, une forte influence sur sa compétitivité par rapport aux conifères. Goldblum & Rigg (2005) ont proposé que l'ES profiterait d'une augmentation de croissance plus importante que l'AB ou encore l'épinette blanche (*Picea glauca*) sous les changements climatiques. Cela pourrait améliorer le statut de l'ES à sa limite nordique. Cependant, d'autres facteurs limitent vraisemblablement l'établissement de l'ES au sein de la forêt boréale tels que l'herbivorie (Salk et al. 2011), la prédation des graines (Hsia and Francl 2009), les insectes et les pathogènes (Cleavitt et al. 2011) ainsi que l'absence d'associations mycorhiziennes arbusculaires, lesquelles sont sensibles aux sols acides (Coughlan et al. 2000). Le déficit en eau pour les semis d'ES devrait aussi être accentué sous les couverts résineux à cause de la plus grande interception de l'eau de pluie par les conifères comparativement aux feuillus (Barbier et al. 2009).

## 0.3 Sensibilité de l'érable à sucre aux déficiences nutritives

L'ES est une espèce particulièrement sensible aux faibles disponibilités de Ca et Mg comparativement aux autres espèces qui se développent sur les sols acides (Kobe et al. 2002, Duchesne and Ouimet 2009, Long et al. 2009). Les sols acides sont classiquement retrouvés sous les conifères, lesquels tendent à diminuer le pH du sol en raison de la nature acidifiante de leur litière comparativement aux feuillus (Augusto et al. 1998). La santé, la distribution et les performances de l'ES sont classiquement contraintes par les faibles disponibilités en Ca et Mg des sols acides, ce peut entraîner des déficiences en Ca et Mg foliaires (van Breemen et al. 1997, Houle et al. 2007, St. Clair et al. 2008, Long et al. 2009, Halman et al. 2013, Halman et al. 2014). La plupart des peuplements en déclin au Québec ont, par exemple, été attribués aux conséquences des pluies acides, ce qui entraîne un excès d'Al et de Mn dans la solution de sol ainsi qu'une faible disponibilité en cations basiques. À moyen terme, on peut y constater des déficiences nutritives foliaires (Duchesne et al. 2002, Ouimet et al. 2006, Duchesne and Ouimet 2009). Les excès d'Al et de Mn dans la solution de sol conduisent généralement à des phytotoxicités qui réduisent la photosynthèse et l'efficience de la carboxylation des feuilles d'ES (St. Clair et al. 2008). Le Ca peut ainsi influencer indirectement le métabolisme primaire et la croissance au travers de son interaction compétitrice et de régulation avec l'Al et le Mn. Il contribue également au bon développement d'endomycorhizes arbusculaires (Jarstfer et al. 1998), ce qui augmente l'acquisition des nutriments (en particulier le P en cas de faible disponibilité) et de l'eau chez l'ES (Ouimet et al. 1996, Augé 2001). Cette symbiose racinaire améliore ainsi la survie, la croissance et la résistance aux stress biotiques et abiotiques de l'ES sur les sols aux faibles pH (Coughlan et al. 2000, Juice et al. 2006). D'autre part, le Mg joue un rôle crucial dans le fonctionnement de la photosynthèse en activant la Rubisco et limite les toxicités du Mn et de l'Al au sein des feuilles au travers d'interactions compétitrices (St. Clair et

al. 2008). Ainsi, des expériences de chaulage sur des peuplements d'ES en déclin ont démontré une augmentation des taux de croissance et de photosynthèse dès l'ajout de 3 Mg $ha^{-1}$ de $CaMg(CO_3)_2$ (Liu et al. 1997, Moore and Ouimet 2006, Schaberg et al. 2006, Moore et al. 2014).

Des déficiences en K provoquant une diminution de la productivité de l'ES ont également été observées sur les sols acides (Ouimet and Fortin 1992, Côté and Camiré 1995). Par exemple, Ouimet et Fortin (1992) ont observé que la croissance et la santé de la canopée de l'ES diminuait linéairement avec les concentrations foliaires en K et qu'une fertilisation en K améliorait la croissance. Toutefois, l'effet des déficiences du K ne semblent pas aussi répandues que pour le Ca et le Mg. Encore peu de liens clairs ont pu être démontrés entre les concentrations foliaires en K et la photosynthèse, la croissance et la survie de l'ES.

Des études démontrent que les concentrations en N foliaire ont une influence sur la réponse photosynthétique de l'ES (Reich et al. 1991) alors que d'autres études n'observent pas d'effet (St. Clair 2004). Les déficiences foliaires en Ca et Mg représenteraient de plus fortes contraintes aux performances photosynthétiques (Liu et al. 1997) avec de possibles co-limitations avec l'N (Ellsworth and Liu 1994). Plusieurs études sur les effets du N foliaire et du sol n'ont pas trouvé de corrélations (ou elles n'ont trouvés que des corrélations faibles) avec la réponse de croissance ou la santé de l'ES (Finzi and Canham 2000, Horsley et al. 2000, Duchesne et al. 2002). Ces effets peuvent être la conséquence d'un sol peu limitant en N et soumis à un lessivage important des cations basique sous l'effet des pluies acides dans l'Est de l'Amérique du Nord.

Le sol au sein des sapinières du Bouclier précambrien est généralement acide et pauvre en cations basiques (pH de 3,65 et capacité d'échange cationique effective de 39,6 $cmol_c\ kg^{-1}$ pour l'horizon organique) (Brais et al. 1995, Bélanger et al. 2006). On peut présumer que la capacité de l'ES à s'installer sous ces conditions doit être

influencée par ses exigences nutritives, limitant ainsi sa compétitivité ; celui-ci est idéalement retrouvé sur des sols au pH allant de 5,5 à 7,3 et ne survit pas sur des pH inférieurs à 3,7 (Godman et al. 1990). En fait, Graignic et al (2014) ont proposé que l'épais horizon organique typique des sols boréaux, classiquement très acides, pauvres en Ca et avec un faible taux de minéralisation de l'N, pourrait limiter la migration nordique de l'ES suivant les changements climatiques en affectant les premiers stades d'établissement des semis.

## 0.4 Risques actuels au sein de la distribution de l'érable à sucre

D'un autre côté, la santé et la vigueur de l'ES sous sa distribution actuelle est menacée par d'autres facteurs, suggérant qu'il risque de subir une contraction de sa distribution. Au Sud de sa distribution, on observe un remplacement progressif mais certain de l'ES par le hêtre d'Amérique (*Fagus grandifolia*, Ehrh. - noté FG par la suite). Par exemple, des échecs de régénération de l'ES ainsi qu'une diminution significative de sa densité en faveur de celle du FG ont été observés dans la forêt d'Hubbard Brook au New Hampshire (Hane 2003), dans les Adirondacks (Jenkins 1997) ainsi que dans le Sud du Québec (Beaudet et al. 1999, Duchesne et al. 2005, Gravel et al. 2011). Tandis que le remplacement de l'ES par le FG est incontestable, les raisons possibles expliquant ce phénomène restent toujours nébuleuses. Certaines études ont proposé que le FG aurait une meilleure performance à l'ombre (Canham 1989) et sous les trouées (Takahashi and Lechowicz 2008) que l'ES. D'autres études suggèrent que ce remplacement est probablement dû aux pluies acides, provoquant une acidification du sol et un lessivage subséquent des cations basiques (Duchesne and Ouimet 2009), et que le FG aurait une meilleure performance sous de telles conditions comparativement à l'ES, lequel est sensible à l'acidité des sols (Kobe et al. 2002, Halman et al. 2014). Une herbivorie préférentielle de l'ES par rapport au FG serait également à prendre en compte, notamment par le cerf de Virginie (*Odocoileus*

*virginianus*) (Marquis and Brenneman 1981, Long et al. 2007). Enfin, des perturbations provoquant le rejet de souche du hêtre (ex. maladie corticale, herbivorie, tempêtes) pourraient maintenir une forte densité de jeunes FG dans le sous-bois (Nyland et al. 2006), ce qui entraînerait un effet d'ombrage au détriment de l'ES (Hane 2003). De plus, la production de composés allélopathiques par la litière du FG pourraient limiter la germination et la croissance des semis d'ES et ainsi expliquer son remplacement (Hane et al. 2003).

## 0.5 Possible accès aux ressources minérales du sol

Si les ressources du sol sont limités, la sélection naturelle des arbres peut être basée sur les traits fonctionnels qui modifient le sol et augmentent en retour la disponibilité des ressources pour eux-mêmes ou la diminue pour leur compétiteurs (Binkley and Giardina 1998). La litière de l'ES est riche en cellulose, peu acide et possède un ratio C:N relativement peu élevé. Ces propriétés permettent une décomposition et un apport de nutriment plus rapide que celle de la litière du FG ou des conifères (Finzi et al. 1998, Preston et al. 2000). Si l'ES migre vers le Nord en réponse aux changements climatiques, la qualité de sa litière pourrait modifier l'habitat pour son propre bénéfice en réorganisant la structure des communautés microbiennes du sol et en augmentant la minéralisation et la disponibilité des nutriments. La litière de l'ES pourrait également augmenter le pH du sol, permettant (1) d'améliorer les chances d'associations symbiotiques mycorhiziennes et conséquemment, (2) d'augmenter l'acquisition des nutriments, l'efficience d'utilisation de l'eau et la résistance aux pathogènes (Read 1991). De plus, certaines espèces d'arbre comme l'ES ont la capacité d'accéder aux ressources des horizons minéraux profonds du sol pour subvenir à leur besoin nutritionnels, tel que le Ca (Blum et al. 2002, Dijkstra and Smits 2002). Certaines espèces relâchent même de grandes quantités d'exsudats racinaires et de $CO_2$ dissout (pour former du $H_2CO_3$), ce qui augmente le taux d'altération des minéraux du sol, libérant Ca, Mg, K et P de la

charpente cristalline des minéraux. Ce processus est influencé par la composition des espèces (la plupart étant des conifères et des espèces de fin de succession – (Quideau et al. 1996, Augusto et al. 2000), la présence de symbioses mycorhiziennes (Hoffland et al. 2004), la croissance rapide (Bélanger et al. 2004) et la minéralogie du sol (Lafleur et al. 2013). L'ES a été sélectionné pour sa tolérance à la compétition racinaire afin d'améliorer l'accès aux ressources du sol (Messier et al. 2009). Par exemple, une étude a suggéré que l'ES avait développé un trait racinaire d'augmentation de la disponibilité du Ca au travers d'un changement de la chimie de sa rhizosphère modifiant les taux d'altération des minéraux afin de satisfaire ses besoin nutritifs, comparativement à AB et le bouleau blanc (*Betula papyfera*) (Séguin et al. 2004). Sous les changements climatiques, ce trait pourrait conférer un avantage à l'ES pour coloniser les sites dont le sol serait considéré « hostile » en comblant le déficit en calcium par l'augmentation du prélèvement du calcium pédologique. Cependant, puisque les exigences nutritionnelles de l'ES pour sa croissance sont élevées, on peut présumer que son incidence par rapport aux conifères sur le recyclage des éléments nutritifs devient l'élément limitant le plus sa progression au sein de la sapinière.

## 0.6 Comparaison de sa tolérance nutritive avec l'érable rouge

Contrairement à l'ES et d'autres espèces forestières, la distribution de l'érable rouge (*Acer rubrum* L., ER) s'est étendue avec succès au cours du dernier siècle sur les sols forestiers acides et pauvres en cations basiques de l'Est de l'Amérique du Nord (Abrams 1998, Alderman et al. 2005, Fei and Steiner 2007). Récemment, Zhang et al (2015) ont observés une augmentation de l'établissement et la croissance de l'ER à la limite nordique de sa distribution. Une étude au sein de l'Allegheny National Forest (Nord-Ouest de la Pennsylvanie) a révélé que les symptômes de

déclins et les taux de mortalité de l'ES étaient trois fois plus élevés que ceux de l'ER (McWilliams 1996). Tandis que ces déclins ont été liés aux faibles disponibilités nutritives du sol et des passages d'insectes ravageurs (Bailey et al. 2004), les raisons du succès de l'expansion de l'ER restent encore incertaines. Les facteurs suggérés dans les études sont aussi variés que le régime de feu, le climat, les interactions biotiques et ses propriétés physiologiques (Warren et al. 2004, Lambers and Clark 2005). Globalement, l'ER a été caractérisé comme un généraliste compétitif qui possèdent à la fois les traits des espèces d'arbre de début et de fin de succession (Abrams 1998). Ainsi, certaines études ont suggéré qu'une plus grande efficience d'utilisation des nutriments foliaires et une plus grande tolérance aux limitations nutritives pourraient expliquer les meilleures performances de l'ER par rapport à l'ES (Abrams 1998, Nagel et al. 2002, St Clair and Lynch 2005). Une comparaison de l'évolution de ses balances nutritives foliaires sur les sols acides des forêts résineuses par rapport à celles de l'ES pourrait donc améliorer notre compréhension des caractéristiques et limites physiologiques de la nutrition de l'ES dans un contexte de changements climatiques.

## 0.7 Plan de thèse

L'objectif général de cette thèse de doctorat a été d'étudier la nutrition et régénération des semis d'ES au sein de sa distribution et en interaction avec des espèces résineuses. Plus spécifiquement, les conditions affectant négativement leur équilibre nutritionnel foliaire et leur survie ont été étudiées, comprenant le climat, les conditions pédologiques ainsi que l'effet du couvert. Ainsi, cette thèse a été divisée en trois chapitres couvrant différents aspects de l'objectif général mentionné.

Le premier chapitre vise à tester l'hypothèse d'un effet négatif global de la présence de conifères sur la nutrition des semis d'ES, quel que soit le site étudié. Pour cela, les concentrations nutritives foliaires de semis d'ES ont été mesurées sur trois

sites représentant le maximum de distribution latitudinal de l'ES au Québec. Spécifiquement, l'effet du climat ainsi que l'effet du sol ont été quantifiés à chaque site. D'autre part, pour chaque site, l'évolution des concentrations nutritives foliaires a été étudiée le long d'un gradient d'enrichissement en espèces résineuses composé de trois types de couvert (dominance feuillue, peuplement mixte, dominance résineuse).

Le deuxième chapitre a pour objectif d'investiguer les facteurs pouvant mener à des échecs de régénération de l'ES au sein de sa distribution au Québec, lié à la présence de hêtre ou celle de conifères. Ce chapitre vise spécifiquement à tester l'hypothèse d'un échec de régénération des semis d'ES causé par (1) une faible disponibilité en lumière et des effets allélopathiques sous le FG ; et (2) un faible pH ainsi qu'une faible disponibilité en nutriments sous les conifères. Pour cela, le chapitre se consacre uniquement sur l'un des sites étudié dans le chapitre précédant, c.à.d. St. Hippolyte dans les Laurentides, au sein duquel un gradient plus détaillé a été mis en place (lequel part d'érablières à hêtre avec présence ou non de régénération d'ES jusqu'à des peuplements résineux avec présence ou non de régénération d'ES). Une expérience de survie a été mise en place à chaque niveau du gradient écologique, comprenant des semis plantés directement dans le sol et d'autres au sein de pots fertilisés, afin d'isoler les effets potentiels du sol et de la lumière sur la régénération de l'ES. Parallèlement, les effets du type de couvert, des conditions du sol, de la lumière et de l'herbivorie ont été testés sur la nutrition et la présence des semis d'ES.

Afin d'apporter des informations complémentaires sur l'écophysiologie de l'ES, le troisième chapitre porte sur une comparaison de l'équilibre nutritionnel foliaire des semis d'ES versus ER. Le concept des balances nutritives foliaires a été utilisé afin de tester l'hypothèse d'une faible acclimatation des balances nutritives foliaires de l'ES par rapport à l'ER, et lié à une plus forte exigence nutritive face à une augmentation de l'abondance en conifères. Il s'agit d'une approche novatrice de diagnostique

foliaire et qui s'avère complémentaire aux analyses des précédents chapitres. À l'aide de transformations en log ratios isométriques, les balances nutritives foliaires permettent de tenir compte des interactions entre nutriments au sein de la feuille et d'éliminer les biais potentiellement crées avec les comparaisons traditionnelles de nutriment bruts.

CHAPITRE I

# CONIFER PRESENCE MAY NEGATIVELY AFFECT SUGAR MAPLE'S ABILITY TO MIGRATE INTO THE BOREAL FOREST THROUGH REDUCED FOLIAR NUTRITIONAL STATUS

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## 1.1 Abstract

The discipline of ecology suffers from a lack of knowledge of non-climatic factors (e.g. plant-soil, plant-plant and plant-insect interactions) to predict tree species range shifts under climate change. The next generation of simulation models of forest response to climate change must build upon local observations of species interactions and growth along climatic gradients. We examined whether sugar maple (*Acer saccharum*) seedlings were disadvantaged with respect to soil nutrient uptake under coniferous canopies, as this species would need to migrate northward into conifer-dominated forests in response to climate change. An experimental design was applied to 3 sites, forming the largest possible latitudinal/climatic gradient for sugar maple in Quebec (Canada) and isolating the effect of conifer presence on its seedling's nutritional status. We tested whether: (1) both soil and climate; and (2) presence of conifers affected foliar nutrient levels of sugar maple seedlings. Climate and soil (through pH) strongly affected nutrient availability for sugar maple seedlings and predicted 62.1% of their foliar nutrient variability. When controlling for site effects, we found a significant negative effect of conifers on foliar Ca and Mg levels of maple seedlings, which can adversely affect their overall health and vigour. When considering projected modifications of the forest environment due to climate change, we suggest that northward migration of sugar maple will be negatively affected by the presence conifers through reduced foliar nutrition.

Key words: *Acer saccharum*, seedlings, foliar nutrition, ecological gradient, calcium, magnesium, species interactions.

## 1.2 Introduction

Climate records indicate that surface air temperatures have increased globally (~0.85 °C) since the late 1800s, and should continue to rise (≥1.5 °C) until the end of the 21st century. due to an increase in radiative forcing (Hartmann et al., 2013). Simulation models also suggest that available moisture and the severity of drought will respectively decrease and increase in the near future in many parts of the world (Dai, 2011; Van Oldenborgh et al., 2013). Such changes in climate are creating physiological constraints that force plant species to find new ecological optima by shifting their ranges to higher elevations and latitudes.

Literature reviews suggest that changes in physiology, phenology, growth and distribution of plants have occurred over the last 30-40 years (Rosenzweig et al., 2008; Chen et al., 2011; Allstadt et al., 2015). Thus far, these changes were most easily observed at the edges of their altitudinal distributions. For example, Beckage et al. (2008) documented a mean progression of 100 m of temperate hardwoods into the altitudinal boreal forest that occurred over the last 40 years in Vermont, USA.

Studies supporting a climate-mediated northward shift in plant species are based almost entirely on modelling. For example, Iverson et al. (2008) simulated habitat shifts of 134 tree species in the eastern United States, with about 50 % gaining habitat and 40 % losing habitat under a conservative climate change scenario. More recently, Zhu et al. (2012) compared present latitudes of seedlings and adult trees in the eastern USA at their range limits as evidence for redistribution. Their results suggest that species may be adapting poorly to climate change, given a lack of evidence for a generalised climate-mediated northward shift and range contraction for some species, which emphasises the need for field studies that assess the impediments to forests that are posed by climate change.

For a tree species to colonise an area with sufficient rapidity to compensate for its projected loss in habitat, it must quickly disperse its seeds over rather long distances and acclimate to conditions other than climate. Seed dispersal rates are known for most Canadian tree species (Clark et al., 1998). However, we have a poor understanding of how trees adapt to new growing environments. When the Wisconsin ice sheets retreated, thus ending the last glaciation, plant species migrated northward into pristine and gradually organising environments (Jackson and Overpeck, 2000). Over centuries, resident ecosystems have developed into complex systems which have led to positive feedbacks in plant communities (Wilson and Agnew, 1992). Positive feedbacks imply that certain species have created conditions in the resident environment (*e.g.*, soil pH, water, nutrient and light availability, allelopathic compounds, fire disturbance, etc.) that increase their competitive advantage, but such conditions complicate the establishment, nutrition, survival and growth of migrating species. Consequently, understanding the effects of resident soils (Lafleur et al., 2010) and resident plant species (Ettinger and HillèRisLambers, 2013) on migrating plants is crucial for predicting plant species redistribution under climate change. Most current models fail to simulate recent forest mortality episodes and species migration rates; they are only calibrated to regional climates and do not consider the reorganisation of interactions and feedback cycles between species and site conditions (Clark et al., 2014).

Sugar maple (*Acer saccharum* Marshall; hereafter, referred to as "maple") and balsam fir (*Abies balsamea* [L.] Miller) coexist within the deciduous-boreal ecotone. The presence of isolated islands of maple beyond its northern range suggests that it is not solely limited by climate (Graignic et al., 2014). However, maple is not dominant in the boreal forest, which means that at the very least climate has reduced its competitiveness relative to conifers. Goldblum & Rigg (2005) proposed that maple has a greater potential for increased growth under climate change at the deciduous-boreal ecotone of Ontario, Canada, than does balsam fir or white spruce (*Picea*

*glauca* [Moench] Voss). This response potential could enhance the future status of maple at its northern limit. Yet, other factors such as herbivory (Salk et al., 2011), seed predation (Hsia and Francl, 2009), insects and pathogens (Cleavitt et al., 2011), and the probable reduction of arbuscular-mycorhizae fungi associations with maple roots, which are sensitive to low soil pH values (Coughlan et al., 2000), must also have limited maple establishment in the boreal forest.

Sugar maple is also a Ca-demanding tree species, and its growth and distribution are likely controlled by soil Ca availability (van Breemen et al., 1997). Graignic et al. (2014) proposed that the nutrient-poor boreal soils characterised by thick litter layers can limit northward maple migration under climate change by affecting its early stages of seedling establishment. In fact, maple declines in eastern North America are linked to low soil Ca availability. Low available Ca concentrations, in turn, can be caused by Ca leaching and imbalances due to high Al and Mn activity in the soil solution (which is induced by atmospheric acid deposition (St. Clair et al., 2008; Long et al., 2009)) as well as exports of Ca in harvested biomass (Bélanger et al., 2002).

The main objective of this study was to determine whether foliar nutrients of maple seedlings are negatively affected when growing under an increasing proportion of coniferous trees at three different latitudes in southern Quebec. The latitudinal responses were a means of assessing the nutritional acclimation potential of maple seedlings to the soil conditions prevailing in the boreal forest. We hypothesised that: (1) both soil and climate would affect foliar nutrient levels of maple seedlings; and (2) foliar nutrient levels, notably Ca, would be adversely affected by the presence of coniferous tree species.

## 1.3 Materials and Methods

### 1.3.1 Study sites

Three sites were identified in southern Quebec for the study, where maple is found with an increasing proportion of conifers. The first was located near Windsor in the Eastern Townships (45°34'N, 71°57'W). The second site was at Station de Biologie des Laurentides (SBL) of the Université de Montréal, which is located in St. Hippolyte (45°59'N, 74°00'W). The third site was at Lac Labelle, which is located in the Abitibi-Témiscamingue region (48°10'N, 79°27'W) (Figure 1.1). These sites form the largest possible latitudinal/climatic gradient for maple in Quebec. The southernmost site, Windsor, lies within the southern limit of the sugar maple-basswood (*Tilia americana* L.) domain. The St. Hippolyte site is located in the sugar maple-yellow birch (*Betula alleghaniensis* Britton) domain of the lower Laurentians. This is the northernmost deciduous forest domain in Quebec, and the St. Hippolyte site is located near its northern limit, at the edge of the deciduous-boreal forest transition (Saucier et al., 2009). In both deciduous domains, windthrow is a major natural disturbance that affects forest dynamics.

The northernmost site, Lac Labelle, is found within the balsam fir-white birch (*Betula papyrifera* Marshall) bioclimatic domain, which is typically dominated by coniferous species (Saucier et al., 2009). Lac Labelle is well outside the natural distribution of maple and, thus, is found only in small islets. The presence of a maple population at this location is exceptional and is likely due to a site history that spared the forest from severe fires. Catastrophic wildfire and insect pest irruptions are the principal disturbances in the fir-birch domain.

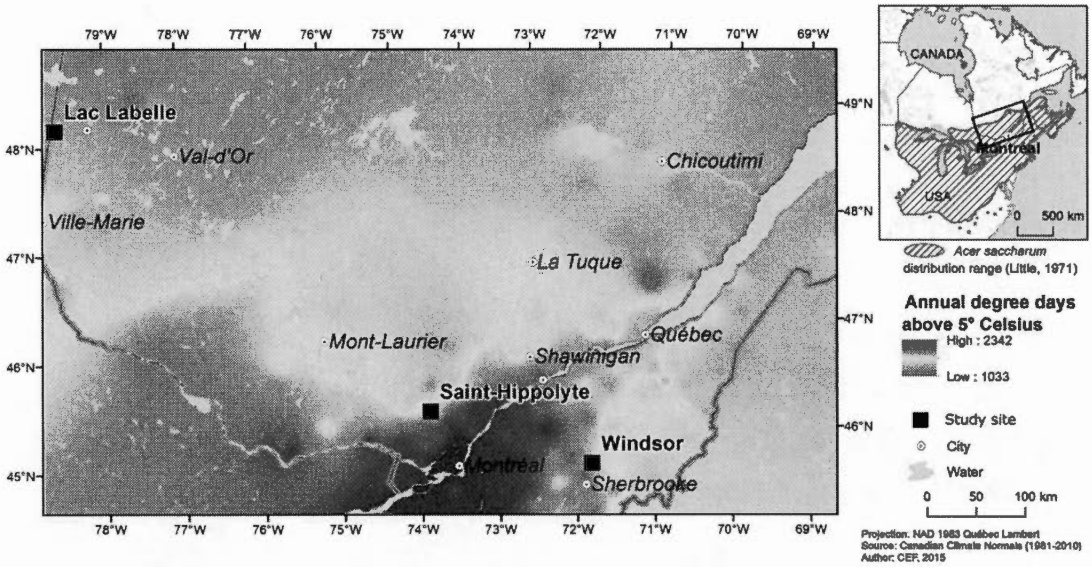


**Figure 1.1** Location of study sites with annual degree days above 5 °C

The BioSIM model (Régnière and Bolstad, 1994) was used to estimate annual degree-days (base 5°C), precipitation, temperature and other climate variables at the three study sites based on the last ten years (2003-2013 period). Model software can be obtained from ftp://ftp.cfl.forestry.ca/regniere/software/BioSIM/. Using site elevation, latitude and longitude, BioSIM uses multiple regressions to extrapolate data from the closest climatic stations. BioSIM yields climatic data that are statistically indistinguishable from measured data (Régnière and St-Amant, 2007). Site coordinates that were used as input data and outputs from BioSIM are presented in Table 1.1. Variation in climate variables that are simulated by BioSIM is associated with the latitudinal range of the three sites. Mean annual temperature, annual degree-days above 5 °C, annual number of frost-free days, and rainfall are similar between the two most southern sites, *viz.*, Windsor and St. Hippolyte, and much higher than the northernmost site, Lac Labelle (Table 1.1).

**Table 1.1** Geographical coordinates, elevations, mean annual degree-days (base 5°C), annual air temperatures, annual precipitation, and annual frost-free days of the study sites.

| Site | Coordinates | Elevation (ms) | Degree days (°D) | Temperature (°C) | Precipitation (mm) | Frost-free days |
|---|---|---|---|---|---|---|
| Lac Labelle | N 48°10'42" W 79°27'24" | 375 | 2188 | 0.5 | 948 | 82 |
| St. Hippolyte | N 45°59'18" W 74°00'20" | 360 | 2845 | 4.9 | 1270 | 153 |
| Windsor | N 45°36'07" W 71°50'43" | 308 | 2919 | 5.1 | 1287 | 164 |

Note: Climate variables are means that were simulated for the 2000 to 2010 period using BioSIM.

## 1.3.2 Experimental design

At each site, foliar nutrient levels of maple seedlings and soil pH, moisture and nutrient availability were examined under an increasing proportion of conifers. Within each site, four plots (50 m × 50 m) were delineated for each of the three forest canopies: (1) hardwood stands of maple and birch; (2) mixed hardwood-conifer stands with maple, birch and conifers; and (3) conifer-dominated stands. Plot selection was based on maple seedlings and saplings presence (3 sites × 3 species compositions × 4 replicates = 36 plots). Species in the conifer-dominated stands varied between sites. The Lac Labelle plots were covered with balsam fir, eastern white cedar (*Thuja occidentalis* L.) and a few white or paper birch trees. In St. Hippolyte, the forest cover consisted of balsam fir, eastern white cedar, eastern white pine (*Pinus strobus* L.), and spruce species, together with a few white or paper birch and red maple (*Acer rubrum* L.). The Windsor site contained balsam fir, eastern hemlock (*Tsuga canadensis* L.), white birch and a few eastern white cedar trees. Basal area of each plot was measured for each tree species present on stems with a

diameter at breast height ≥ 9 cm. Appendix A shows the percentage contributions of each species to total basal area by forest types.

In each plot, maple leaves were sampled in early August of 2013 from five seedlings after recording their total height at ground level. During the same period, samples of the forest floor and upper B horizons (first 15 cm) were collected from the soil profile at five different locations within each plot. Ion-exchange resin sticks, i.e., Plant Root Simulators (PRS$^{TM}$, Western Ag, Saskatoon, SK, Canada), were used to assess ionic activity, namely $NO_3^-$, $NH_4^+$, $H_2PO_4^-$, $Ca^{2+}$, $Mg^{2+}$, $K^+$, $Al^{3+}$, $Fe^{3+}$ and $Mn^{2+}$. The cationic or anionic resin in these probes consists of a thin membrane (surface area = 1.5 cm × 5.5 cm) that is encased in a thin plastic support (3 cm × 15 cm). Three pairs of cation and anion probes were inserted vertically to a depth of 10 cm into the B horizon at random locations within each plot with minimal disturbance to the overlying forest floor. They were installed in early June 2013 and collected 8 weeks later. Rather than a static measurement at a particular point in time that is provided by conventional soil extraction methods, PRS probes can be deployed in a manner that allows for dynamic measurements of ions flowing through the soil over time. They are now being frequently used in forest ecology research (Hangs et al., 2004; Moukoumi et al., 2012; Bilodeau-Gauthier et al., 2013).

Topsoil volumetric water content (VWC, $\Theta_v$) and temperature over the 2013 growing season (May to September) were monitored respectively with soil moisture sensors (Waterscout SM100, Spectrum Technologies Inc., Plainfield, IL, USA) and multifunctional probes (Waterscout SMEC 300 SM/EC/T, Spectrum Technologies) installed at the three sites. Sensors were buried at depths of 10 and 20 cm, and connected to a data logger (WatchDog 1650 Micro Station, Spectrum Technologies). The instruments were set to record data every 6 hours. Finally, each plot was characterised by recording topographic and vegetative data such as elevation, slope, aspect and tree density.

### 1.3.3 Foliar and soil analysis

Upon arrival in the laboratory, specific leaf area (SLA) was determined following the procedures of Pérez-Harguindeguy et al. (2013) for plant functional traits. Leaves were weighted and surface area was measured using the WinFOLIA™ software (Regent Instruments Inc., Quebec City, QC, Canada). Leaf samples were then oven-dried (65 °C for 72 h), weighed and finely ground using a planetary ball mill (Vibratory Micro Mill Pulverisette 0, Fritsch GmbH, Idar-Oberstein, Germany). The pulverised samples were analysed for total C and N using high temperature (1040 °C) combustion and infrared detection (EA 1108 CHNS-O Analyser, Thermo Fisons, Waltham, MA, USA). For Ca, Mg, K, Mn and P determination, a ground subsample was digested for 4 h at 100 °C in 15N $HNO_3$ (0.2 g leaf:2 ml $HNO_3$). Base nutrient and Mn levels were determined using atomic absorption/emission spectroscopy (model AA-1475, Varian, Palo Alta, CA, USA), whereas P levels were determined colorimetrically (molybdenum blue) on a continuous flow analyser (Technicon Instruments Corp., Tarrytown, NY, USA).

Soil samples were air-dried and sieved to pass a 2 mm-mesh to remove coarse fragments. Particle size distributions of upper B horizon samples were determined from sub-samples using a laser particle analyser (Partica LA-950, Horiba Instruments, Irvine, CA, USA). Giving the high organic content of some B horizon samples, they were treated by loss-on-ignition before particle size measurement. Soil pH was measured in water (1:5 soil:water) for forest floor and B horizon samples. Exchangeable concentrations of $Ca^{2+}$, $Mg^{2+}$, $K^{+}$, $Al^{3+}$ and P-$PO_4^{3-}$ of forest floor and B horizon samples were determined using the Mehlich III extraction procedure described by Ziadi et al. (2007). Base nutrients and Al levels were determined using atomic absorption-emission and P-$PO_4^{3-}$ levels were determined colorimetrically as indicated above for foliar analysis. Forest floor and B horizon samples were finely ground for total C and N determination using the EA 1108 CHNS-O analyser.

After they were removed from the soil, the PRS probes were thoroughly cleaned of soil with deionised water. Cleaned probes were placed into zipseal bags and refrigerated until analysis. Pairs of PRS probes for each plot were eluted for 1 h with 0.5 M HCl to remove adsorbed ions from the resin membrane. Both $NH_4$-N and $NO_3$-N were determined colorimetrically by continuous flow analysis (Autoanalyser III, Bran & Luebbe, Buffalo, NY). Concentrations of $Ca^{2+}$, $Mg^{2+}$, $K^+$, P-$H_2PO_4^-$, $Fe^{3+}$, $Al^{3+}$, $Mn^{2+}$, $Cu^{2+}$, $Zn^{2+}$, $SO_4^{2-}$ and $B(OH)_4^{3+}$ were determined by inductively coupled plasma atomic emission spectroscopy (ICP-AES, Optima 3000-DV, PerkinElmer Inc., Shelton, CT, USA).

### 1.3.4 Statistics

Data were analysed using the statistical software package R version 3.0.0 (R Core Team, 2013). Descriptive statistics were used to characterise each site, and to compare soil and foliar nutrients between forest types within site. For the sake of comparison between methods, simple Pearson correlation coefficients were also determined between values of respective nutrients (Ca, Mg, K and P) or Al as determined by the PRS probes and Mehlich III extraction. Due to similar trends observed using the two methods (see Appendix B), the discussion is focused on PRS probes data only.

Principal Component Analysis (PCA) was used to reduce the dimensionality of the data, and to visualise variation in soil properties and foliar nutrients between sites and forest types. Prior to analysis, data were normalised (centered and scaled) as required for multivariate analysis. Ordinations provided a visual assessment of the structure of the data as a whole, *i.e.*, whether plots could be grouped by sites or forest types.

One-way ANOVA was used to test the significance of differences in the dependent variables among sites or between forest types. This was followed by means separations using Tukey's HSD (honest significant difference) tests. Assumptions of normality and homoscedasticity of residuals were verified prior to analysis, and data were transformed when necessary.

Variation partitioning was used to quantify individual parts of the explained foliar nutrient variation by selected groups of explanatory variables obtained by forward selection. The forward selection of explanatory variables was first performed using the *forward.sel* function in the *packfor* package (Dray et al., 2013) after testing for multi-collinearity within the matrices (using calculation of variance inflation factors). Variation partitioning was then performed using the *varpart* function in *vegan* (Oksanen et al., 2013) and represented schematically by Venn diagrams. Significance of each partition was determined by permutation testing using partial redundancy analysis (*rda* function available in the *vegan* package) and ANOVA.

Linear mixed-effect models were developed using the *lme* function in the *nlme* package (Pinheiro et al., 2014) to test the effect of forest types on foliar nutrients, with sites and plots being included as random factors. Normality of residuals was tested and transformations were performed when necessary. Differences between forest types were determined with Tukey's HSD tests using the *glht* function in the *multcomp* package (Hothorn et al., 2008). Predicted values and standard errors of the mixed models were computed using the *predictSE* function in the *AICcmodavg* package (Mazerolle, 2015).

All coefficients of determination ($R^2$) that were obtained from the aforementioned analyses, and which were reported in this study as a means of explaining variation in the data set, are adjusted $R^2$ values, hereafter denoted as $R^2_a$. $R^2_a$ is the unbiased form of the coefficient that takes into account the number of input variables in the model. It is required when performing variation partitioning (Peres-

Neto et al., 2006). When not provided directly by the analysis or function, $R^2_a$ was calculated with the *RsquareAdj* function in the *vegan* package.

## 1.4 Results

### 1.4.1 Site differences in soil properties

Analysis of soil physical and chemical properties confirmed their clear partitioning by site (Figure 1.2). Average soil pH (FH-horizon) ranges from 4.2 to 4.7, with St. Hippolyte being the most acidic, followed by lac Labelle and Windsor. Mineral soils (upper B horizons) at all sites have low clay content (< 5.4 %) with a relatively small range (< 3 %) (Table 1.2). In contrast, silt content varied from 40 % in St. Hippolyte to 60 % in lac Labelle. As a whole, St. Hippolyte has coarser textured upper B horizons, with sand content averaging 57 %. Soil solution ionic activities that were recorded by PRS probes differ substantially between sites (Table 1.2) and are likely due to variations in soil texture, organic carbon levels and mineralogy. Soil solution $NO_3^-$ and $NH_4^+$ (hereafter referred to as N), Ca, Mg and Al activities are higher in Windsor and St. Hippolyte than in Lac Labelle (Table 1.2). Despite the small range in clay content, significant negative correlations ($r$ ranging from -0.398 to -0.526, $P < 0.05$) were found with soil solution N, Ca, Mg and Al activity (results not shown). Also, clay content and mean annual temperature were strongly correlated ($r = -0.761$, $P < 0.001$; results not shown), suggesting a site effect on nutrient dynamics that is mediated by the confounding effects of climate and soil.

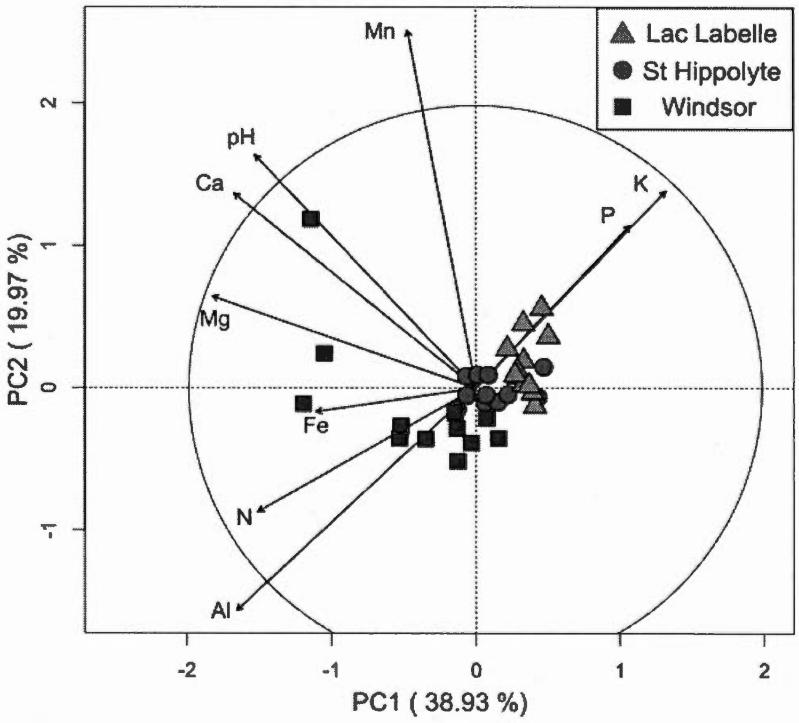


**Figure 1.2** Principal component analysis (PCA) of soil pH and soil solution ionic activities as measured by PRS probes. The circle of equilibrium contribution is provided. Variables that have a longer vector than this radius make a higher contribution than average and can be interpreted with confidence.

**Table 1.2** Physical and chemical properties of the forest floor and B horizon as a function of study sites and forest types (H: hardwood stands, Mx: mixed hardwood-conifer stands, C: conifer-dominated stands) within each site.

| Site | Cover | FH horizon | | | B horizon | | |
|---|---|---|---|---|---|---|---|
| | | pH | VWC | Temperature | Clay | Silt | Sand |
| | | | | °C | % | % | % |
| Lac Labelle | - | 4.39 ± 0.03 | 14.90 ± 1.42 | 14.36 ± 0.04 | 5.41 ± 0.09 | 60.40 ± 0.95 | 34.20 ± 1.01 |
| St. Hippolyte | - | 4.24 ± 0.03 | 17.17 ± 0.48 | 15.97 ± 0.10 | 2.69 ± 0.17 | 39.94 ± 1.49 | 57.37 ± 1.64 |
| Windsor | - | 4.72 ± 0.10 | 11.19 ± 3.38 | 16.10 ± 0.02 | 2.90 ± 0.10 | 56.63 ± 1.49 | 40.47 ± 1.58 |
| Lac Labelle | H | 4.55 ± 0.06 | - | - | 5.74 ± 0.12 | 60.00 ± 1.51 | 34.25 ± 1.64 |
| | Mx | 4.41 ± 0.05 | - | - | 5.45 ± 0.15 | 63.04 ± 0.82 | 31.50 ± 0.94 |
| | C | 4.23 ± 0.06 | - | - | 5.02 ± 0.17 | 58.13 ± 2.21 | 36.83 ± 2.31 |
| St. Hippolyte | H | 4.40 ± 0.05 | - | - | 2.75 ± 0.45 | 46.07 ± 3.74 | 51.16 ± 4.19 |
| | Mx | 4.29 ± 0.06 | - | - | 2.83 ± 0.16 | 39.72 ± 0.91 | 57.44 ± 1.04 |
| | C | 4.05 ± 0.03 | - | - | 2.48 ± 0.21 | 34.02 ± 1.43 | 63.49 ± 1.55 |
| Windsor | H | 5.05 ± 0.17 | - | - | 2.72 ± 0.16 | 54.28 ± 2.59 | 42.99 ± 2.73 |
| | Mx | 5.02 ± 0.21 | - | - | 3.13 ± 0.24 | 59.84 ± 3.02 | 37.02 ± 3.23 |
| | C | 4.11 ± 0.16 | - | - | 2.85 ± 0.12 | 55.75 ± 2.01 | 41.40 ± 2.12 |

Note: Soil volumetric water content (VWC) and temperature are means for the June-August period. Means are presented with standard errors.

**Table 1.2** (continued)

| Site | Cover | Soil solution ionic activities (µg/10cm/2month) | | | | |
|---|---|---|---|---|---|---|
| | | N | P | K | Ca | Mg |
| Lac Labelle | - | 12.5 ± 0.63 | 3.10 ± 0.83 | 217 ± 39.3 | 264 ± 32.1 | 73.1 ± 8.06 |
| St. Hippolyte | - | 22.6 ± 17.5 | 2.68 ± 1.10 | 67.6 ± 11.1 | 739 ± 87.5 | 131 ± 11.6 |
| Windsor | - | 81.2 ± 17.0 | 0.31 ± 0.10 | 31.4 ± 10.2 | 666 ± 203 | 162 ± 31.0 |
| Lac Labelle | H | 13.3 ± 1.42 | 5.10 ± 2.10 | 218 ± 66.9 | 223 ± 65.5 | 76.3 ± 15.0 |
| | Mx | 12.9 ± 0.76 | 2.33 ± 0.58 | 289 ± 91.7 | 300 ± 56.2 | 83.3 ± 15.4 |
| | C | 11.3 ± 0.98 | 1.88 ± 0.90 | 142 ± 22.3 | 269 ± 54.0 | 59.8 ± 12.5 |
| St. Hippolyte | H | 59.3 ± 51.8 | 1.08 ± 0.36 | 63.8 ± 22.6 | 964 ± 134 | 143 ± 12.9 |
| | Mx | 4.17 ± 0.88 | 2.73 ± 1.21 | 64.8 ± 12.6 | 535 ± 118 | 109 ± 26.6 |
| | C | 4.34 ± 0.58 | 4.22 ± 3.17 | 74.0 ± 25.6 | 718 ± 147 | 141 ± 19.2 |
| Windsor | H | 117 ± 41.2 | 0.51 ± 0.24 | 38.5 ± 29.0 | 993 ± 335 | 217 ± 74.0 |
| | Mx | 70.2 ± 23.4 | 0.31 ± 0.17 | 14.8 ± 6.79 | 846 ± 460 | 189 ± 38.8 |
| | C | 55.9 ± 15.4 | 0.10 ± 0.04 | 40.9 ± 10.6 | 159 ± 18.0 | 79.2 ± 7.63 |

| Site | Cover | Soil solution ionic activities (µg/10cm/2month) | | |
|---|---|---|---|---|
| | | Mn | Al | Fe |
| Lac Labelle | - | 46.5 ± 7.14 | 18.2 ± 2.63 | 7.74 ± 1.57 |
| St. Hippolyte | - | 9.55 ± 2.43 | 55.3 ± 15.4 | 6.04 ± 1.12 |
| Windsor | - | 28.9 ± 19.1 | 136 ± 17.9 | 49.1 ± 12.2 |
| Lac Labelle | H | 43.0 ± 13.4 | 24.3 ± 3.43 | 12.0 ± 2.87 |
| | Mx | 60.6 ± 3.60 | 19.6 ± 5.31 | 7.65 ± 2.37 |
| | C | 35.7 ± 16.1 | 10.6 ± 1.97 | 3.57 ± 1.19 |
| St. Hippolyte | H | 15.2 ± 6.02 | 96.5 ± 40.9 | 6.67 ± 2.44 |
| | Mx | 5.35 ± 2.39 | 33.3 ± 4.19 | 5.60 ± 1.66 |
| | C | 8.10 ± 2.37 | 36.0 ± 8.46 | 5.84 ± 2.22 |
| Windsor | H | 9.84 ± 2.80 | 165 ± 28.6 | 22.4 ± 4.69 |
| | Mx | 69.1 ± 56.5 | 128 ± 45.8 | 68.8 ± 32.2 |
| | C | 7.82 ± 2.56 | 116 ± 12.7 | 56.1 ± 14.2 |

### 1.4.2 Site differences in foliar nutrients

Levels of foliar nutrients in maple seedlings vary significantly between sites (Table 1.3). Seedlings in Windsor have higher foliar Ca and Mg levels than the two other sites, while St. Hippolyte, in turn, has higher foliar Ca and Mg than Lac Labelle. Similarly, Windsor and St. Hippolyte have similar foliar N levels, whereas their levels are higher than Lac Labelle. As a whole, foliar nutrients decrease with increasing latitude. Foliar Mn levels are higher in Lac Labelle than those at the two other sites, and foliar Mn levels in Windsor are higher than those in St. Hippolyte. Foliar Ca/Mn and Mg/Mn ratios decrease with increasing latitude. Specific leaf area of maple seedlings vary significantly between sites, with Windsor having the highest values, followed by Lac Labelle and St. Hippolyte (Table 1.3).

### 1.4.3 Relationship between foliar nutrients, soil and climate

A forward selection of significant variables that best explained foliar nutrients of maple seedlings was first performed after removing collinearity between variables. The most robust model was composed of annual number frost-free days, soil pH, and soil solution P and Mn activities, which explained 62.1 % of the variation in foliar nutrients of maple seedlings ($P < 0.001$).

**Table 1.3** Foliar nutrient levels, ratios of calcium and magnesium to manganese and specific leaf area (SLA) of sugar maple seedlings as a function of study sites and forest types (H: hardwood stands, Mx: mixed hardwood-conifer stands, C: conifer-dominated stands) within each site.

| Site | Cover | C | N | P | K | Ca | Mg |
|---|---|---|---|---|---|---|---|
| | | | | mg/g | | | |
| Lac Labelle | - | 469.8 ± 1.01 | 16.17 ± 0.28 b | 1.07 ± 0.05 | 5.21 ± 0.28 b | 5.05 ± 0.23 c | 1.33 ± 0.06 c |
| St. Hippolyte | - | 467.4 ± 1.56 | 18.15 ± 0.39 a | 1.10 ± 0.02 | 6.28 ± 0.23 a | 8.32 ± 0.23 b | 1.88 ± 0.08 b |
| Windsor | - | 471.0 ± 1.00 | 18.63 ± 0.34 a | 1.20 ± 0.05 | 5.77 ± 0.21 ab | 11.27 ± 0.46 a | 2.67 ± 0.06 a |
| | H | 469.8 ± 1.53 | 15.66 ± 0.53 | 1.17 ± 0.09 | 4.74 ± 0.65 | 4.63 ± 0.36 | 1.36 ± 0.10 |
| Lac Labelle | Mx | 470.0 ± 1.83 | 16.05 ± 0.30 | 1.00 ± 0.10 | 4.74 ± 0.47 | 5.20 ± 0.45 | 1.27 ± 0.10 |
| | C | 469.6 ± 1.91 | 16.79 ± 0.52 | 1.04 ± 0.06 | 5.51 ± 0.30 | 5.31 ± 0.31 | 1.35 ± 0.08 |
| | H | 467.9 ± 2.61 | 18.81 ± 0.60 | 1.13 ± 0.04 | 6.28 ± 0.41 | 9.11 ± 0.34 a | 2.14 ± 0.16 a |
| St. Hippolyte | Mx | 466.9 ± 1.20 | 17.07 ± 0.56 | 1.06 ± 0.03 | 6.02 ± 0.43 | 8.40 ± 0.38 ab | 1.92 ± 0.12 ab |
| | C | 467.4 ± 3.44 | 18.57 ± 0.80 | 1.12 ± 0.03 | 6.53 ± 0.37 | 7.44 ± 0.36 b | 1.58 ± 0.12 b |
| | H | 475.1 ± 2.02 | 17.14 ± 0.55 b | 0.98 ± 0.10 b | 4.83 ± 0.34 b | 11.24 ± 0.78 a | 2.62 ± 0.14 ab |
| Windsor | Mx | 468.4 ± 1.83 | 18.83 ± 0.51 ab | 1.47 ± 0.06 a | 5.75 ± 0.38 b | 12.72 ± 1.02 a | 2.84 ± 0.10 a |
| | C | 468.8 ± 1.24 | 20.35 ± 0.69 a | 1.13 ± 0.04 ab | 7.05 ± 0.37 a | 9.38 ± 0.50 b | 2.51 ± 0.08 b |

| Site | Cover | Mn | Ca/Mn | Mg/Mn | Ca/Mg | SLA |
|---|---|---|---|---|---|---|
| | | mg/g | | | | $mm^2/mg$ |
| Lac Labelle | - | 1.85 ± 0.12 a | 3.66 ± 0.37 b | 1.01 ± 0.11 b | 4.09 ± 0.22 b | 3.24 ± 0.08 b |
| St. Hippolyte | - | 1.02 ± 0.07 c | 11.24 ± 1.14 a | 2.52 ± 0.26 a | 4.87 ± 0.24 a | 2.26 ± 0.05 c |
| Windsor | - | 1.35 ± 0.11 b | 14.64 ± 2.02 a | 3.31 ± 0.40 a | 4.20 ± 0.14 b | 4.02 ± 0.24 a |
| | H | 2.01 ± 0.23 | 3.14 ± 0.48 | 0.98 ± 0.20 | 3.52 ± 0.25 | 3.15 ± 0.10 |
| Lac Labelle | Mx | 1.88 ± 0.17 | 3.41 ± 0.56 | 0.86 ± 0.17 | 4.52 ± 0.45 | 3.11 ± 0.17 |
| | C | 1.68 ± 0.22 | 4.43 ± 0.81 | 1.17 ± 0.21 | 4.23 ± 0.41 | 3.46 ± 0.10 |
| | H | 0.96 ± 0.13 | 15.27 ± 2.17 a | 3.04 ± 0.49 a | 4.61 ± 0.30 | 2.28 ± 0.09 |
| St. Hippolyte | Mx | 0.99 ± 0.14 | 12.33 ± 2.42 ab | 2.82 ± 0.55 a | 4.58 ± 0.25 | 2.27 ± 0.07 |
| | C | 1.10 ± 0.10 | 8.12 ± 0.87 b | 1.71 ± 0.22 b | 5.43 ± 0.58 | 2.22 ± 0.08 |
| | H | 1.20 ± 0.18 b | 13.86 ± 1.99 b | 3.32 ± 0.47 b | 4.36 ± 0.22 a | 4.36 ± 0.52 |
| Windsor | Mx | 0.80 ± 0.11 b | 25.15 ± 4.80 a | 5.32 ± 0.92 a | 4.46 ± 0.33 a | 3.54 ± 0.47 |
| | C | 2.04 ± 0.12 a | 4.89 ± 0.30 c | 1.30 ± 0.07 c | 3.78 ± 0.15 b | 4.19 ± 0.13 |

Note: Means are presented with standard errors. Different letters between sites and forest types (within columns) indicate a statistically significant difference at $P < 0.05$ (permutation paired *t*-test).

Secondly, variation partitioning was conducted to explain foliar nutrients of maple seedlings using variables that were selected by forward selection (see Venn diagram, Figure 1.3A). Climate, through mean annual frost-free days, explained as much as 40 % of total variation in foliar nutrients. This is almost twice the variation that was explained by soil properties (21.7 %), i.e., forest floor pH and soil solution Mn and P activities. The overlap of the variation explained by both climate and soil was quite small and negative ($R^2_a$ = -0.016). A second partitioning of the variance was tested using soil properties alone, with climate variables being replaced by soil texture (see Venn diagram, Figure 1.3B). This model explained 49 % of the variation in foliar nutrients. Clay content and soil chemical composition (*i.e.*, pH and solution Mn and P activities) explained respectively 23.5 % and 20.7 % of the variation. Because strong correlations were found between soil texture and climate variables, a third partitioning was performed to explore the link between these variables and foliar nutrients of maple seedlings (Figure 1.3C). This partitioning of the variance was tested using soil solution ionic activities as a first component, clay content as a second, and climate as a third. This model explained 61.4 % of total variation in foliar nutrients, and suggests that the variation explained by soil texture is encompassed by the variation that is explained by climate.

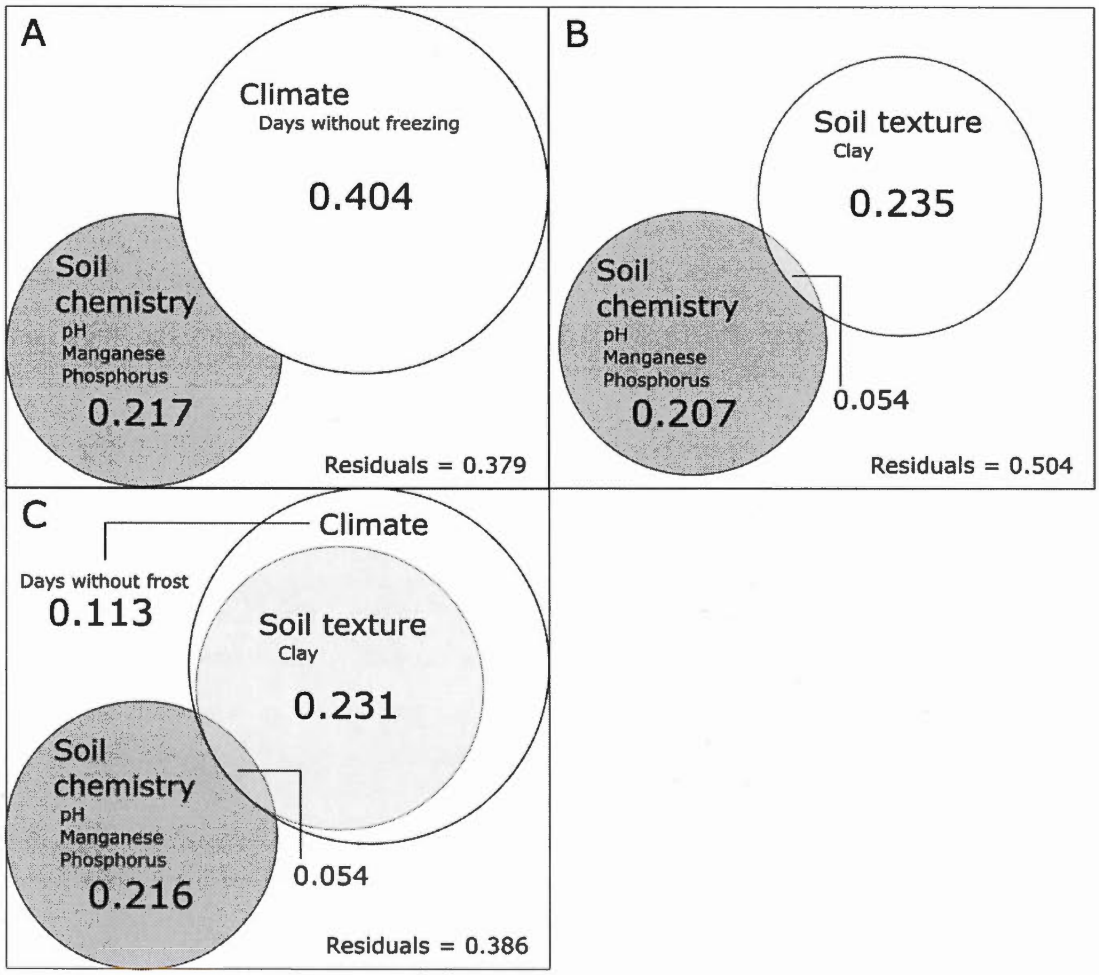


**Figure 1.3** Venn diagrams of foliar nutrients of sugar maple seedlings explained by: (A) soil chemistry and climate variables ($R^2_a$ = 0.621), (B) soil chemistry and soil texture ($R^2_a$ = 0.496), and (C) soil chemistry, soil texture and climate variables ($R^2_a$ = 0.614). Main fractions are proportional between each other and significant at $P < 0.001$. Overlap of main fractions in A was negative ($R^2_a$ = -0.016) and may be explained as a null or hierarchical relationship (Legendre & Legendre 2012).

### 1.4.4 Effect of coniferous species within sites on foliar nutrients

Considering the site effect on soil properties and, in turn, on foliar nutrients of maple seedlings, it was necessary to use a mixed-model analysis to isolate the site effect. Sites and plots, therefore, were used as hierarchical random variables, with forest type as the fixed factor of foliar nutrients. Specific leaf area varies significantly between sites and presents high variability between forest types in Windsor and Lac Labelle. In an attempt to consider differences in light environment between covers, it was therefore preferred to express foliar nutrient levels as unit of leaf area instead of as unit of mass. At the landscape level (*i.e.*, all sites), results of the mixed-model analysis show that foliar Ca and Mg levels of maple seedlings differed between forest types, with hardwoods and mixed hardwood-conifer stands having significantly higher levels than conifer-dominated stands (Figure 1.4A). Moreover, foliar Ca/Mn and Mg/Mn ratios of maple seedlings under conifer-dominated stands are significantly lower than those of seedlings under hardwoods and mixed hardwood-conifer stands (Figure 1.4B). At the site scale, only maple seedlings in Lac Labelle have similar foliar nutrient levels among forest types (Table 1.3). In Windsor and St. Hippolyte, maple seedlings under conifer-dominated stands have significantly lower foliar Ca and Mg levels than under hardwoods. Conversely, maple seedlings under conifer-dominated stands in Windsor exhibit significantly higher foliar N, K and Mn levels than seedlings under hardwoods. Also in Windsor, foliar P levels as well as Ca/Mn and Mg/Mn ratios of maple seedlings under hardwoods are lower than seedlings under mixed hardwood-conifer stands (Table 1.3).

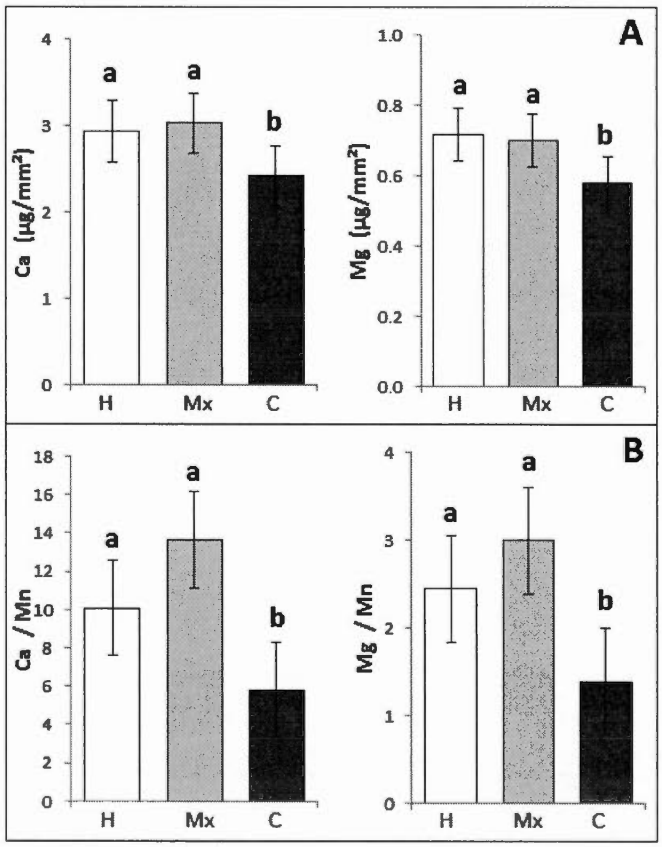


**Figure 1.4** Foliar calcium and magnesium in sugar maple seedlings presented in (A) absolute concentration values and (B) as ratios with manganese under three forest types (H: hardwood stands, Mx: mixed hardwood-conifer stands, C: conifer-dominated stands) as examined by mixed model analysis using sites and plot as random factors. Differences between letters are Tukey's HSD at $P < 0.05$.

## 1.5 Discussion

In this study, we examined foliar nutrient status of maple seedlings at three sites at very different latitudes with each site presenting an increasing proportion of coniferous trees. The objective was to assess the nutritional acclimation potential of maple seedlings to soil conditions prevailing in the boreal forest. Results support our two hypotheses, that is, both soil and climate affect foliar nutrient levels of maple seedlings, and foliar nutrient levels are adversely affected by the presence of coniferous tree species.

### 1.5.1 Site effect on climate, soil and foliage

The clear partitioning of soil pH and solution ionic activity between sites (Figure 1.2) may be more related to soil texture variation than climate, given that the differences were not necessarily reflected by a decrease in these variables with increasing latitude (Table 1.2). The soil at the northernmost site (Lac Labelle) differed from the others due to its higher clay content (Table 1.2). The three sites are located in distinct bioclimatic domains, which are supposedly characterised by contrasting soil resources. Colder, conifer-dominated forests in the north usually generate more acidic soil conditions and lead to lower microbial activity and slower organic matter decomposition than warmer deciduous temperate forests in the south of the province (Binkley and Fisher, 2012). Thick forest floors that are produced in northern forests should lead, therefore, to significant organic matter buildup and low soil nutrient availability, especially N (Binkley and Giardina, 1998).

Our foliar data suggest that nutrient levels in maple seedlings, *viz.*, N, P, Ca and Mg, generally decrease with increasing latitude and decreasing air temperature (Table 1.3). This global pattern of foliar nutrition at our sites suggests that microbial activity, mineralisation of organically bound nutrients in the forest floor, soil nutrient availability, and uptake by trees are indeed impacted by north-south air and soil

temperature gradients of the experimental design (Tables 1.1 and 1.2). Foliar nutrient levels of maple seedlings indicate that soil nutrient availability is normally lower under colder conditions and increasing conifer abundance. The higher clay content in Lac Labelle, differences in mineralogy (not measured) between sites, and the various forest types that were considered in this analysis are likely masking a similar pattern for soil pH and solution ionic activities at the landscape scale.

Results of variation partitioning suggest that climate and soil variables are both important components that affect foliar nutrition of maple seedlings (Figure 1.3A). On the one hand, explained variation that was shared by both groups of variables is negative and can be interpreted as a null relationship or a hierarchical structure of climate over soil variables (Legendre and Legendre, 2012). On the other hand, climate variables and soil texture were found to be highly correlated, suggesting some confounding effect between site and soil. The hierarchical structure of climate over soil pH is rational considering that soil microbial activity and nutrient turnover or availability are temperature-dependent (Zak et al., 1999). Effects of climate and soil on sugar maple regeneration have been demonstrated in other studies (Cleavitt et al., 2011; McCarragher et al., 2011; Graignic et al., 2014). While a confounding effect between climate and soil is apparent, the individual effect of climate on foliar nutrients of maple seedlings is undoubtedly large in our study (Figure 1.3).

Levels of foliar nutrients in maple seedlings (Table 1.3) that were measured in Windsor and St. Hippolyte are within the range that has been reported in other studies of maple seedlings growing on similar acidic soils (*e.g.,* St. Clair & Lynch, 2005a; Park & Yanai, 2009). St. Clair and Lynch (2005a) examined maple seedlings growing on acidic soils (pH 3.7-4.6), while Park and Yanai (2009) studied responses of mature maple trees and seedlings in two sites with contrasting pH (4.1 *vs* 5.4) and soil base cation availability. To our knowledge, however, the levels of foliar N, Ca and Mg that were measured in seedlings from the northernmost site, Lac Labelle, are below

reported literature values for maple seedlings. For example, the mean Ca level of maple seedling foliage at this site is 5.05 mg $g^{-1}$. Considering that Ca values that have been reported for unproductive or declining mature maple stands are between 4 and 6 mg $g^{-1}$ (Ellsworth and Liu, 1994; Wilmot et al., 1996; Moore and Ouimet, 2006), our results suggest that seedlings in Lac Labelle are near or below the threshold for Ca deficiency. In addition, foliar Mn levels of maple seedlings at Lac Labelle and of seedlings under conifer-dominated stands in Windsor are above the reported Mn range for healthy maple trees, i.e. 0.632 - 1.630 mg $g^{-1}$ (Kolb and McCormick, 1993). In Lac Labelle, the high foliar Mn levels are likely the consequence of the high Mn activity in the soil solution (Table 1.2).

The fact that plots under conifers in Lac Labelle have higher soil pH than similar plots in St. Hippolyte as well as higher soil solution Ca activity at the root-soil interface compared to similar coniferous plots in Windsor (Table 1.2) suggests that other mechanisms are controlling maple seedling Ca availability and uptake. This could be due to temperature-dependent mechanisms that would lower nutrient uptake by roots, given that soil temperature is known to affect ion uptake by plants, both directly and indirectly (Pregitzer and King, 2005). For example, an increase in soil temperature can lead to an increase in root growth (Pregitzer et al., 2000; Rogiers et al., 2014), photosynthetic capacity (Schwarz et al., 1997; Wu et al., 2012; Rogiers and Clarke, 2013) and rates of nutrient uptake by fine roots (Dong et al., 2001; Pregitzer and King, 2005). Also, air and soil temperatures have been demonstrated as a major factor determining the length of the growing season (Körner and Basler, 2010). Therefore, we can consider maple seedlings at the northernmost site generally experience a shorter growing season (see air and soil temperatures in Tables 1.1 and 1.2), which likely means less effective acquisition of nutrients (Nord and Lynch, 2009). For instance, because Ca is taken up in the transpiration stream, warmer sites (with more transpiration) should have a greater potential for Ca uptake.

The low foliar N, Ca and Mg levels that were measured in maple seedlings from Lac Labelle (Table 1.3) could suggest that this northern maple provenance has developed a more conservative nutritional strategy. At this site, the persistence of a maple population is exceptional. The maple population in Lac Labelle is well outside its natural distribution and found only in small islets. This site is mostly occupied by coniferous species that have presumably conditioned the environment for a very long time towards their own benefit (through soil pH and nutrients, water and light availability, allelopathic compounds, among other factors). In accordance with the concept of positive feedbacks in plant communities, these modifications complicate the establishment of migrating species (Wilson and Agnew, 1992). Maple seedlings in Lac Labelle have passed through centuries of adaptation to grow and persist in this harsh and cold environment, far beyond its natural bioclimatic domain. One manifestation of this adaptive phenotypic plasticity may involve lower nutrient levels in foliage (Valladares et al., 2007) relative to the more southern maple provenances.

### 1.5.2 Effect of coniferous species

Decreases in foliar Ca levels and Ca/Mn ratios of maple seedlings with an increasing proportion of conifers were observed at the landscape level (Figure 1.4), suggesting that an increase in conifers has a negative effect on nutrient uptake of maple seedlings. Maple is particularly sensitive to low Ca and high Mn availability in comparison to other species growing on acidic soils (St. Clair and Lynch, 2005b; Long et al., 2009). Positive correlations have been found between growth and Ca nutrition of maple seedlings, saplings and trees (Kobe et al., 2002; Huggett et al., 2007; Halman et al., 2013; Halman et al., 2014), whereas negative correlations have been found between maple tree health and foliar Mn levels (Houle et al., 2007; Horsley et al., 2000). Increasing activity of Mn in the soil solution may potentially induce foliar Ca (and Mg) deficiencies through strong competitive interactions (St. Clair et al., 2008). Calcium can influence primary metabolism and growth indirectly

through its interaction with other nutrients. Although N and P are the two most important nutrients limiting tree growth worldwide (Vitousek, 2004), the health and vitality of maple appears to be constrained by Ca availability on acidic soils where foliar values are below deficiency thresholds (Drohan et al., 2002; Houle et al., 2007; St. Clair et al., 2008; Long et al., 2009). Moreover, higher rates of growth were recorded in studies that surveyed the effect of liming on declining maple stands (Liu et al., 1997; Moore and Ouimet, 2006; Schaberg et al., 2006; Moore et al., 2014). Most of the declines could be attributed partly to soil acidification by acid deposition, resulting in low availability of soil base cations. The negative influence of conifers on foliar Mg levels and Mg/Mn ratios (Figure 1.4) of maple seedlings is not marginal because Mg deficiencies can exert large effects on forest health and decline in acidic soils. For example, foliar Mg levels were negatively correlated with health declines of maple stands (Horsley et al., 2000). Manganese can impair photosynthetic functions of maple as it competes with Mg for activating Rubisco – however, Mn only has a fraction of the activation potential of Mg (St. Clair et al., 2008). In acidic soils, the mobility of Mn reaches its optimum below pH 5 (Havlin et al., 2005). Conifers tend to decrease soil pH relative to most hardwoods due their more acidic litters (Augusto et al., 2000). Hence, our results also imply that the abundance of conifers negatively influences the health of maple seedlings by reducing soil pH and Ca and Mg availability (Table 1.2 and Figure 1.4).

The effect of conifers on foliar nutrition of maple seedlings was not observed individually at the northernmost site (Table 1.3), which may be explained by physiological acclimation and a threshold response. Species composition for each forest type in Lac Labelle differs from the two southernmost sites. Hardwood stands were rarely found without at least one conifer tree in the surrounding stand, whereas finding maple seedlings in the conifer-dominated stands was a greater challenge compared to the southernmost sites. The lower seedling density in conifer-dominated

stands suggests that only the most robust seedlings were able to survive and grow, or that seedlings were able to survive and grow because they benefited from more suitable microsites. Therefore, the effects of conifers on maple seedling nutrition are conservative because the seedlings that were sampled in those plots were presumably among the fittest. Moreover, maple seedlings in Lac Labelle exhibited the lowest foliar nutrient levels among the three sites (Table 1.3) as well as with respect to the literature, and it showed higher foliar Mn levels than reported values for healthy maple trees. This was the case whether the seedlings were growing under hardwoods or conifers. Hence, we propose maple seedlings that were found under hardwoods in Lac Labelle were at or near a nutritional threshold that jeopardises their survival.

Foliar N levels of maple seedlings in Windsor increased with increasing proportions of coniferous species (Table 1.3). This result is surprising, given that soil solution N activity tends to decrease under conifer-dominated stands. Many of the hardwood stands in Windsor, however, had an abundance of ferns in the understorey (62.5 ±7.2 % of ground vegetation cover), which is believed to have been favoured by past forestry practices. Ferns are less present in the conifer-dominated stands (18.3 ±6.6 % of ground vegetation cover). In fact, maple stands in this region of southern Quebec are frequently invaded by ferns, particularly hay-scented fern (*Dennstaedtia punctilobula* [Michaux] T.Moore), which is a result of canopy opening due to natural disturbances and harvesting (Groninger and McCormick, 1992; Engelman and Nyland, 2006; Ouimet et al., 2016). We believe that competition for N between ferns and maple seedlings explains the lower N levels in maple foliage (Momen et al., 2105).

### 1.5.3 Ecological implications

Results from this study emphasise the importance of climate and interactions with other dominant species with respect to the foliar nutrition and regeneration of

maple seedlings, a field of research that is still poorly studied and elucidated (Cleavitt et al., 2014). Our results are consistent with evidence that important factors other than climate must be included to improve our abilities to forecast tree species range shifts under climate change (McMahon et al., 2011; Brown and Vellend, 2014; Graignic et al., 2014; Zhang et al., 2015). For example, Zhang et al. (2015) found that regeneration and growth of red maple at its northern limit in Quebec were more strongly controlled by fire return intervals than climate.

It should be reminded that the measured maple seedlings in this study were those capable of growing naturally, even under stressful conditions encountered beneath conifers. The results of the study are likely to represent only the best conditions that were experienced by maple seedlings growing under coniferous trees. The study especially underscores the negative effects of both low soil pH and conifer presence on foliar nutrition of maple seedlings. This negative effect could be an important factor limiting northward shifts of maple populations in Quebec under climate change. The range of current maple populations in the south, in fact, is threatened with ongoing contraction under climate change. Increasing temperatures would not provide immediate benefits to maple for several reasons: (1) available moisture and drought severity are projected to decrease and increase respectively in the near future (Houle et al., 2012; Collins et al., 2013; Walsh et al., 2014); (2) freeze-thaw events are likely to increase due to reductions in snow depth, which could result in root mechanical injuries (Bertrand et al., 1994; Decker et al., 2003; Comerford et al. 2013); and (3) increased rates of soil nitrification due to increased soil temperatures. The last two processes, in turn, would lead to soil acidification by exacerbating $NO_3^-$, Mg and Ca leaching (Fitzhugh et al., 2003), followed by decreasing foliar N, Ca and Mg levels (Pilon et al., 1994).

Maple trees in the south are currently enduring competition exclusion by American beech (Hane, 2003; Duchesne and Ouimet, 2009). Previous modelling

studies that were mostly based on climate suggest a high potential for northward migration of maple (Kellman, 2004; Goldblum and Rigg, 2005). Therefore, we propose that the local soil conditions maintained by coniferous species, i.e. expressed by low Ca and Mg availability, may be one factor among many that limit maple seedling establishment and survival.

Understanding the effect of resident soils (Lafleur et al., 2010) and resident plant species (Ettinger and HilleRisLambers, 2013) on migrating plants is critical for predicting plant species redistribution under climate change. In the boreal forest, more suitable soil conditions are expected in the long-term with climate warming because increased soil temperature will release large amounts of nutrients that were immobilised in organic matter, mostly in the forest floor. Further, migrating deciduous species with high litter quality will alter the soil favourably, at least to some extent. Yet, we can expect that some soil factors will create a substantial time lag in maple range expansion. In addition to competitive exclusion of maple in the south, the worst-case scenario is that maple distribution in Quebec will suffer range contraction in the near future. Thus, further research is needed to elucidate maple acclimation to climate change and new resident environments that are characterised by different soil pH, moisture, nutrient and light availability, allelopathic compounds and disturbances, among others. The presence of predator or pathogen species and the absence of facilitators (*e.g.,* mycorrhizae) in the resident environments also have the potential to decrease the colonisation success of migrating species (Guisan and Thuiller, 2005).

## 1.6 Conclusion

Results from this study indicate that foliar nutrition of sugar maple seedlings is strongly influenced by climate, soil conditions and the presence of dominant coniferous trees. First, as we hypothesised, soil conditions and nutrient availability

influence foliar nutrient levels of maple seedlings. This effect can be mediated by combining effects of soil texture and latitudinal conditions influencing nutrient cycling and soil nutrient availability. In addition, results support our second hypothesis that coniferous species have a negative effect on foliar nutrition of maple seedlings through reductions in foliar Ca and Mg, which are recognised as important for the health and vigour of maples in eastern North America. This negative effect of coniferous species on maple nutrition occurs independently of latitudinal location and soil texture. Establishment and persistence of maple seedlings in the boreal forest of Quebec is less likely than has been suggested in previous studies. While more suitable boreal soil conditions are expected in the long-term due to climate warming, conifer-dominated stands might not provide favourable sites for possible northward maple expansion. More globally, this paper emphasises the need to consider non-climatic factors (*e.g.*, interactions between species and acclimation to soil conditions) in the migratory environment when studying population dynamics in the context of climate change and tree species range shift predictions.

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CHAPITRE II

# BEECH AND CONIFER PRESENCE NEGATIVELY AFFECT THE REGENERATION CAPACITY OF MAPLE SEEDLINGS IN TEMPERATE FORESTS OF EASTERN NORTH AMERICA

Chapter not submitted yet

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## 2.1 Abstract

Understanding tree recruitment dynamics in various growth environments is essential for a better assessment of tree species' adaptive capacity to climate change. We investigated the microsite factors influencing regeneration and foliar nutrition of sugar maple seedlings (*Acer saccharum*) along a gradient of tree species that reflect the change in composition from temperate hardwoods to boreal forests of eastern North America. We specifically tested if the presence of American beech (*Fagus grandifolia*) or the increasing abundance of conifers in the forest negatively affect the light environment, soil chemistry as well as survival and foliar chemistry of naturally and pot-planted maple seedlings. On the one hand, the results indicate that the presence of beech repress sugar maple regeneration by creating an environment with low light availability. On the other hand, under conifer-dominated stands, lower soil pH, accelerated dissolution of some minerals, lower temperature and moisture and higher levels of phenolic compounds have rendered the microsites less suitable for sugar maple regeneration and early seedling growth. This study has identified key microsite factors created by the presence of beech and conifers that may impede the potential of sugar maple to maintain its current range or expand its range northward under climate change.

Key words: Beech, conifers, survival, light availability, soil acidity, mineral weathering, phenols, soil microclimate.

## 2.2 Introduction

Temperate tree species at their northern range are faced with a rapidly changing climate that could provide opportunities for expanding their range northward (Parmesan and Yohe 2003, Rosenzweig et al. 2008, St. Clair et al. 2008, Chen et al. 2011). The shifts in tree species distributions are expected to be particularly large for populations at the limits of their distribution ranges (Iverson et al. 2004). The distribution of plant species is mainly determined by climatic factors, soil properties, light availability and biotic interactions (e.g. browsing, pathogens, invading weeds), which, in combination, constrain the survival and development of the populations (Whittaker 1970, Woodward 1987, Gaston 2009). While many studies observed slower shifts in plant species distribution than climate change itself (Parmesan and Yohe 2003, Loarie et al. 2009, Chen et al. 2011, Zhu et al. 2012), more and more studies suggest that non-climatic factors such as soil properties and biotic interactions as exemplified above are slowing down the migration ability of plant species (McMahon et al. 2011, Brown and Vellend 2014, Graignic et al. 2014, Collin et al. 2016).

Tree recruitment dynamics within new growth environments, including seed germination and seedling survival and adaptation to growth, are poorly understood. Yet, this seems essential for a better assessment of tree species recruitment and sustainability in environments receiving new species in the context of climate change (Gaston 2009, Cleavitt et al. 2014). On the one hand, positive-feedbacks in plant communities (Wilson and Agnew 1992) imply that certain species have created conditions in the resident environment to their benefit and to the disadvantage of migrating plant species. Those conditions can be as varied as acidic soil conditions, low water status, limited soil nutrient and light availability, allelopathic toxin production and microbe-plant associations that can be harmful to other plants (Binkley and Giardina 1998). Some tree species are also more prone to frequent fires,

which can be a disadvantage for other tree species (Wirth 2005). On the other hand, some plant species have developed strategies to augment soil nutrient access and uptake, which likely gives them an advantage over other species. For example, some tree species have the capacity to access deep mineral soil sources to satisfy nutrient demand (Blum et al. 2002, Dijkstra and Smits 2002). Some tree species may even release large amounts of organic acid exudates from their roots and dissolved $CO_2$ (to form $H_2CO_3$), thus promoting soil mineral weathering and the release of Ca, Mg, K and P from the crystal lattices of minerals. This latter process is influenced by species composition (mostly conifers and late succession species – (Quideau et al. 1996, Augusto et al. 2000)), colonization of their roots by mycorrhizal fungi (Hoffland et al. 2004), fast growth (Bélanger et al. 2004) and soil mineralogy (Lafleur et al. 2013).

Over centuries, resident environments have developed into complex biochemical systems that may not always be welcoming to migrating species in terms of their establishment, survival, nutrition and growth. Interactions and feedback cycles between species and site conditions may explain the actual failure of most models to simulate species migration rates as they are most often only calibrated to regional climates (Clark et al. 2014). Understanding the effects of resident soils (Lafleur et al. 2010) and resident species (Ettinger and HilleRisLambers 2013). It thus seems crucial to consider interaction and feedback cycles for the prediction of plant species redistribution under climate change.

Sugar maple (*Acer saccharum* Marsh., hereafter referred to as "maple") is of particular interest given the current challenge facing its recruitment and sustainability at both its northern and southern limits in eastern North America. It is proposed that the acidic soil conditions associated with the conifer dominated boreal forest will limit the northward migration of maple under climate change (Graignic et al. 2014). The growth and survivorship of maple is particularly sensitive to acidic and nutrient-poor soils (St. Clair et al. 2008). Most of the declining maple stands in eastern North America were related to soil acidification and base cation imbalances caused by acid

rain, subsequently leading to foliar Ca and Mg deficiencies and crown decline (Duchesne et al. 2002, Kobe et al. 2002, Juice et al. 2006, Long et al. 2009). Hence, acidic and nutrient-poor soils with thick forest floors (characterized by low N mineralization rates) generally found in the boreal forest of the Precambrian Shield (Moore et al. 1999, Trofymow et al. 2002) may negatively affect early stages of maple seedling establishment, thus limiting its migration potential into the boreal forest. The negative effect of coniferous canopies on foliar nutrient status (mostly Ca and Mg) of maple seedlings was demonstrated in Quebec, independently of latitude (Collin et al. 2016 - see Chapter I). Moreover, maple in its southern distribution limit is currently experiencing a competitive exclusion by American beech (*Fagus grandifolia* Ehrh., hereafter referred to as "beech") (Hane 2003, Duchesne and Ouimet 2009, Gravel et al. 2011). While progressive beech expansion over maple is indisputable, the causes remain unclear. Some studies suggest that beech can perform better than maple in deep shade (Canham 1989), in canopy openings (Takahashi and Lechowicz 2008) and on base cation poor soils (Kobe et al. 2002, Halman et al. 2014), but recent studies done in western Quebec found very little differences in growth response due to liming or light opening among the two species (Bannon et al. 2015, Nolet et al. 2015). Preferential browsing of maple by animals (e.g. deer) and insects has also been observed; hence, lowering its competitive ability relative to beech (Marquis and Brenneman 1981, Long et al. 2007). Forest disturbances (e.g. ice storms, pathogens) is another factor that favours beech over maple through suckering, which results in a high beech sapling density that negatively affects maple regeneration through shading (Hane 2003). Finally, the production of toxic (allelopathic) compounds from beech litter was proposed as a competitive disadvantage for maple regeneration (Hane et al. 2003).

The objectives of this study were to investigate the factors influencing regeneration and foliar nutrition of maple seedlings under the absence and presence

of beech or conifers. We tested the following general hypothesis: the presence of beech in the canopy of deciduous forest areas and the presence or dominance of coniferous species in the canopy of other parts of the forest negatively affects the survival of maple seedlings. More specifically, we hypothesized that survival and foliar nutrition of maple seedlings are negatively affected by (1) low light availability, high concentrations of phenolic compounds in the soil and increased herbivory under beech canopies; and (2) lower soil pH and nutrient availability under conifer canopies.

## 2.3 Material and Methods

### 2.3.1 Study site

The study site is located at the *Station de Biologie des Laurentides* (SBL) of the *Université de Montréal* in St. Hippolyte, Quebec (45°59'N; 74°00'O), 80 km North of Montreal. Thirty-year average precipitation at SBL is 1100 mm, with 30% falling as snow. Mean annual temperature is 3.6 °C. The SBL is found at the transition with the boreal forest, within the northern limit of the maple-yellow birch (*Betula alleghaniensis* Britton) bioclimatic domain of the lower Laurentians (Saucier et al. 2009). Due to its geographic position and history of frequent fires, the area has developed into a mosaic of tree species. Maple is found concomitantly with red maple (*Acer rubrum* L.), yellow birch, poplars (*Populus spp.* L.), balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* Moench) and northern white cedar (*Thuja accidentalis* L.). It was therefore possible to find a gradient of forest tree species that reflect the change in composition from the southern hardwood to the northern boreal forest of Quebec, which included plots with no maple regeneration at the extremes of the ecological gradient (i.e. pure hardwoods and conifer-dominated stands). The soils are Orthic Humo-Ferric Podzols with a sandy loam texture (Soil Classification Working Group, 1998). The forest floor is a moder humus form of 5 to

10 cm. They were developed from rocky glacial till derived in part from the underlying anorthosite pluton of the Morin series (Doig, 1991), but due to the small size of the pluton, the soils have a mineral composition that also reflects the mixture of more felsic rocks (e.g. charnockite, mangerite, syenite) in the surroundings of the anorthosite which were mixed by continental ice sheets during the Pleistocene (Bélanger et al. 2012).

### 2.3.2 Experimental design

Four plots (50 × 50 m) of each of these seven forest canopies were delineated: (1) hardwood stands of maple and beech without maple regeneration, (2) hardwood stands of maple and beech with some maple regeneration, (3) hardwood stands of maple and birch spp., (4) mixed hardwood-conifer stands with a higher dominance of hardwoods, (5) mixed hardwood-conifer stands with a higher dominance of conifers, (6) conifer-dominated stands with maple seedlings, and (7) conifer-dominated stands with at least one maple tree present but with no maple regeneration (7 species composition × 4 repetitions = 28 plots). Basal area of each plot was measured for each tree species present on stems ≥ 9 cm in diameter at breast height so that the percentage contributions of all species to total basal area of the plot could be calculated individually (see Table 2.1). The percent contributions of hardwoods and conifers to total basal area were also computed individually.

**Table 2.1** Total basal area of the various forest types studied and individual contributions by species.

| | SMBe-nr | SMBe | SMBi | MH | MC | C | C-nr |
|---|---|---|---|---|---|---|---|
| Basal area (m²/ha) | 32.5 b | 32.5 b | 37 ab | 31.5 b | 28.25 b | 50 a | 53.33 a |
| Individual contribution to basal area by species (%) | | | | | | | |
| *Acer saccharum* | 61.75 | 62.5 | 69 | 24.75 | 3.25 | 1.75 | 0 |
| *Acer rubrum* | 0 | 0 | 0 | 9.75 | 15.25 | 3.5 | 6.67 |
| *Betula papyfera* | 3.75 | 3.75 | 2.25 | 40 | 25.75 | 24.75 | 16.67 |
| *Betula alleghaniensis* | 0 | 0 | 22.5 | 0 | 0 | 0 | 0 |
| *Fagus grandifolia* | 32.5 | 31.75 | 4 | 2.5 | 1.25 | 0 | 0 |
| *Populus grandidentata* | 0 | 0 | 0 | 13.5 | 3.5 | 0 | 0 |
| *Abies balsamea* | 2 | 2 | 2.25 | 9.5 | 28 | 12.5 | 20.67 |
| *Pinus strobus* | 0 | 0 | 0 | 0 | 14 | 16.5 | 0 |
| *Picea sp* | 0 | 0 | 0 | 0 | 3.5 | 15.25 | 0 |
| *Thuja occidentalis* | 0 | 0 | 0 | 0 | 5.5 | 13.25 | 20.33 |
| *Tsuga canadensis* | 0 | 0 | 0 | 0 | 0 | 12.5 | 35.67 |
| Contribution to basal area by general taxa (%) | | | | | | | |
| Hardwoods | 98 | 98 | 97.75 | 90.5 | 49 | 30 | 23.34 |
| Conifers | 2 | 2 | 2.25 | 9.5 | 51 | 70 | 76.67 |

Different letters indicate a statistically significant difference for basal area at $P < 0.05$. Percent contributions by individual species were not tested. SMBe is maple-beech stands, SMBi is maple-birch stands, MH is mixed hardwood-conifer stands with dominance of hardwoods, MC is mixed hardwood-conifer stands with dominance of conifers, C is conifer-dominated stands, and nr is no maple regeneration.

### 2.3.3 Seedlings and foliage

In each plot, maple leaves were sampled in early August of 2013 from five naturally growing seedlings after recording their morphology (i.e. total height and diameter at the ground level). Upon arrival in the laboratory, the leaves were weighed and surface area was measured using the WinFOLIA$^{TM}$ software (Regent Instruments Inc., Quebec City, QC, Canada). WinFOLIA$^{TM}$ was also used to compute a proxy for herbivory. The software allows calculating the surface of holes that were created by herbivores relative to the total leaf area, i.e. the "damaged" areas were reported as a percentage of the total leaf area). This was further used as a percentage of minimum observed herbivory for comparison between forest types.

Leaf samples were then oven-dried for 72 h at 65°C, weighed and finely ground using a planetary ball mill (Vibratory Micro Mill Pulverisette 0, Fritsch GmbH, Idar-Oberstein, Germany). Ground subsamples were then used for C and N determination using combustion and infrared detection (EA 1108 CHNS-O Analyzer, Thermo Fisons, Waltham, MA, USA). For Ca, Mg, K and P determination, subsamples (0.2 g) of the pulverized leaf tissue were also digested in glass test tubes with 2 ml of concentrated $HNO_3$ for 4 h at 100°C. Concentrations of Ca, Mg and K were then determined using atomic absorption/emission (model AA-1475, Varian, Palo Alta, CA, USA), whereas P concentration was analyzed colorimetrically (molybdenum blue) with a Technicon Auto-Analyzer (Technicon Instruments Corporation, Tarrytown, NY, USA).

Chlorophylls and carotenoids were extracted using the protocol described in Minocha et al. (2009). We used ethanol as a reliable solvent. Three leaf disks (3.5 to 5.5 mg in total) were taken for each sampled seedling and placed in 2 mL microfuge tubes (Eppendorf Safe Lock, Eppendorf North America, Westbury, NY). One and a half milliliters of 95% ethanol were then added to each tube and placed in a water

bath to incubate at 65°C for 2 h in full darkness. Heated samples were removed from the water bath and centrifuged for 5 min at 13 500 *g*. Finally, aliquots were placed in spectrophotometer polystyrene cuvettes (1 mL capacity, Sigma-Aldrich®, Saint-Louis, MO) and absorbance was recorded at 470, 649 and 664 nm with a Hitachi spectrophotometer (Hitachi Ltd., Tokyo, Japan). Concentrations of chlorophyll *a* and *b* and total carotenoids were calculated using the equations of Lichtenthaler (1987) that were reported by Minocha et al. (2009).

### 2.3.4 Survival experiment

A survival experiment was also conducted in the plots with the specific goal of identifying the factors explaining maple regeneration failure under maple-beech and conifer-dominated stands. Two-year old bare root maple seedlings (*Ministère des Forêts, de la Faune et des Parcs* tree nursery, Berthier, Quebec, Canada) varying in size from 25 to 45 cm were planted in each plot. Two types of planting were made to isolate the effects of soil chemistry from the effects of light availability on seedling survival. First, five seedlings were directly planted in the natural soil using a planting shovel. Second, three seedlings were planted into 4 L pots filled with a mix (1:3 ratio) of local mineral soil and a premium potting mix (PRO-MIX®, Rivière-du-Loup, QC, Canada) containing peat, perlite, limestone and the MicoActive™ organic growth enhancer (i.e. vesicular-arbuscular mycorrhizae). The soil mixture was also fertilized twice during the growing season with a fertilizer for trees (N: 8%, $P_2O_5$: 2%, $K_2O$: 2%, Mg: 1.5%, Ca: 8%, S: 5%, Fe: 0.3%; McInnes Natural Fertilizers Inc, Stanstead, QC, Canada), thus providing the nutrients required for maple seedling growth. To ensure that the seedlings in the pots were growing under the same light conditions as the seedlings planted in the natural soil, pots were completely buried in the ground so that all seedlings were growing at the same level. In total, 224 maple seedlings were planted, i.e. 140 in natural soil and 84 in pots. All seedlings were marked with numbered flags and were left to grow for two full growing seasons (May 2013 to

September 2014). Total height was recorded at planting on all seedlings and at final sampling in September 2014 only on the seedlings that survived. Seedlings were surveyed 5 times during the experiment for browsing, survival and total height. Unfortunately, 6 seedlings planted in pots were uprooted by animals during the summers of 2013 and 2014 in 2 plots and 1 plot, respectively. These were eliminated from our survival and growth computations.

### 2.3.5 Light availability

Three hemispherical photographs were taken in all sample plots and at different places in July 2014 at 1 m aboveground to characterize light availability in each sampling area. We used a Fujifilm Finepix S 4600 digital camera (Fujifilm Corporation, Tokyo, Japan) that was equipped with a hemispherical Fisheye Converter FC-E8 lens, which was itself mounted on a Fotodiox lens mount adapter (Nikon to Canon EOS). In total, 84 pictures were taken and analyzed with a GNU Image Manipulation Program (GIMP v 2.8 software; http://www.gimp.org/). Pixels constituting the sky were isolated from pixels constituting the canopy and reported as a percentage of total pixels in the picture. This measurement was further defined as the percentage of canopy openness, which is the percentage of open sky seen from beneath a forest canopy.

### 2.3.6 Soils

Soil volumetric water content (VWC) was monitored both in natural and artificial (pots) soils during the 2013 growing season (i.e. monthly between May and September, five measurements per soil type per plot) at a depth of 7.5 cm using a FieldScout TDR 300 Soil Moisture Meter (Spectrum Technologies Inc., Aurora, IL, USA). Soil temperature was recorded for a full year (i.e. May 2013 to May 2014) using temperature data loggers (Thermochron® iButtons, model DS1921G, Maxim

Integrated Products Inc., Sunnyvale, CA, USA). A total of 56 temperature data loggers were distributed among the plots (i.e. one in the soil and one in a pot), buried at a depth of 10 cm and set to record data every 6 hours. At the end of one year, loggers were retrieved to extract the data. Finally, environmental data such as elevation, slope, exposure and tree basal area were noted to characterize each plot.

Soil samples of FH and upper B horizons were also collected during the 2013 growing season at five different locations within each plot. Upon arrival in the laboratory within 12 h, the samples were air-dried before sieving with a 2 mm mesh to remove any coarse fragments. Giving the high organic content of some mineral soils, subsamples of all B horizon samples (≤ 2 mm) were treated by loss on ignition (850°C) before analysis of particle size distribution using the Horiba Partica LA-950 Laser Particle Analyzer (Horiba Instruments, Irvine, CA, USA). Soil pH was measured in water using a 1:5 soil to water ratio for both the FH and B horizon samples. Forest floor and B horizon subsamples were also finely ground for determination of organic C and total N using the EA 1108 CHNS-O Analyzer.

Ion-exchange resin [i.e. Plant Roots Simulator (or PRS$^{TM}$) probes (Western Ag Innovations, Saskatoon, SK, Canada)] were used to assess the soil solution ionic activity (notably $NO_3^-$-N, $NH_4^+$-N, $H_2PO_4^-$-P, $Ca^{2+}$, $Mg^{2+}$, $K^+$, $Al^{3+}$, $Fe^{3+}$ and $Mn^{2+}$). Within each plot, three pairs of cation and anion probes were randomly inserted vertically under the FH horizon at a depth of 10 cm in early June of 2013. Care was taken to insert the probes with as little disturbance as possible. Probes were finally collected 8 weeks later. The PRS$^{TM}$ probes is an improved method compared to conventional extractions of soils sampled at a particular point in time as they allow for a dynamic measurement of ions flowing through the soil over time, and are now being frequently used for forest ecology research (Hangs et al. 2004, Moukoumi et al. 2012, Bilodeau-Gauthier et al. 2013). In the laboratory, the PRS$^{TM}$ probes were thoroughly cleaned free of soil with deionized water, placed into zipseal plastic bags

and stored in the fridge until analysis by Western Ag Innovations. Pairs of PRS$^{TM}$ probes for each plot were submitted to 1 h elution with 0.5 M HCl to remove the adsorbed ions from the resin membranes. Ammonium ($NH_4^+$-N) and $NO_3^-$-N were determined colorimetrically on a segmented flow Autoanalyzer III (Bran and Luebbe Inc., Buffalo, NY, USA), whereas $Ca^{2+}$, $Mg^{2+}$, $K^+$, $H_2PO_4^-$-P, $Fe^{3+}$, $Al^{3+}$, $Mn^{2+}$, $Cu^{2+}$, $Zn^{2+}$, $SO_4^{2-}$-S and $B(OH)_4^{3+}$-B were determined by Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-AES, PerkinElmer Optima 3000-DV, PerkinElmer Inc., Shelton, CT, USA).

Free phenols were monitored by placing three polyester N-free bags (50 μm porosity; ANKOM Technology, Macedon, NY, USA) per plot. The bags were filled with 1 g dry weight of XAD-7 resin (Rohm and Hass, Philadelphia, PA, USA) and were placed under the FH horizon. They were allowed to remain in the field for a 2-month period (July and August 2013). Upon collection, resin bags were returned to the laboratory where they were frozen at -20°C until analysis. Total phenols in resin bags were analyzed following a sequential extraction with water followed by 50% aqueous methanol (Morse et al. 2000). Each capsule was placed in a polypropylene centrifuge tube with 30 ml of distilled water and shaken for 30 min. The aqueous fraction was later decanted into a glass vial and frozen at -20°C until analysis. The resin was then immersed in 10 ml of 50% aqueous methanol and shaken for 30 min. Extracts were decanted into clean glass vials and the process repeated two additional times to create a total extraction volume of 30 ml. The methanol extracts were stored at -20°C until analysis. Total phenol analysis was performed using the modified Prussian blue technique to give greater color stability (Graham 1992) and measured against appropriate phenolic standards (0.001 M gallic acid) at 700 nm with the Hitachi spectrophotometer.

Finally, we performed a sequential chemical leaching procedure proposed by Lafleur et al. (2013) on podzolic B horizons sampled in each plot (5 per plot) as a

means to determine the concentration of exchangeable (i.e. adsorbed on exchange surfaces) and non-exchangeable (i.e. within the crystal lattice of minerals) base cations. This approach can also be used to selectively dissolve minerals and in turn, determine assemblages of minerals in the soil when a more complete chemical analysis of the leaches is performed, e.g. total P (Bélanger et al. 2012). Specifically, organic matter was first removed from the soil by loss on ignition. Three g of that soil was thoroughly washed several times with nanopure water to remove the excess ash which can contain high amounts of nutrients, notably base cations. Exchangeable cations adsorbed onto the soil exchange complex were then extracted with 30 ml of 1 M $NH_4Cl$ solution for 2 h on an end-over-end shaker. The intermediate step consisted in a leach performed for 2 h on the end-over-end shaker with 30 ml of 0.1 M HCl. The 0.1 M HCl leach attacks the most easily weathered minerals, thus releasing nutrients from minerals such as free calcite and epidote and some apatite (Drouet et al. 2005, Nezat et al. 2007). The final leach was performed again for 2 h on the same shaker with 1 M $HNO_3$. The 1 M $HNO_3$ leach attacks more resistant minerals, thus releasing nutrients from minerals such as apatite, biotite and hornblende and some K-feldspars (Nezat et al. 2007, Bélanger and Holmden 2010). Each extract/leach was filtered and stored in the fridge until analysis. The extracts and leaches were analyzed for Ca, K, Na and P using the same equipment and methods as indicated above (see section on foliar nutrient analysis). The results were used to assess base cation levels within the crystal lattice of assemblages of minerals (operationally-defined as susceptible vs. less susceptible to weathering).

### 2.3.7 Statistical analyses

Data were analyzed using the statistical software package R version 3.0.0 (R Core Development Team, 2013). Descriptive statistics were used to characterize each forest type, to compute correlation and linear regression coefficients of determination (r or $R^2$) between foliar and soil variables, and to compare foliar and soil variables

between forest types. Linear mixed-effect models were used in an attempt to consider the blocking structure of the experimental design (with plots being included as random factors) in order to test the significance of differences between the measured variables (foliar, soil, etc.) among forest types. This was followed by means separations using Tukey's HSD (honest significant difference) tests. Normality of residuals was verified prior to analysis, and data were transformed when necessary. Analyses were developed using the *lme* function in the *nlme* package (Pinheiro et al. 2014) and Tukey's HSD tests were performed using the *glht* function in the *multcomp* package (Hothorn et al. 2008).

Linear discriminant analysis (LDA) was used to confirm that forest types have different soil properties. For doing so, the multivariate homogeneity of variances within groups was first tested using the *betadisper* function available in the *vegan* library (Oksanen et al. 2013). The LDA was then performed on normalized data with the *lda* function from the *MASS* package and using forest type as a grouping factor. In order to test if all observations were correctly classified among forest types, a posteriori analysis of correct classification was done using the *predict* function available in the *vegan* library.

Redundancy analysis followed by variation partitioning was used to explain the variation in foliar nutrients by explanatory variables (e.g. soil chemistry and particle size distribution, canopy openness, tree basal area) and quantify their individual contributions to the total explained variation. Analyses were respectively used on normalized data with the *rda* and *varpart* functions, both available in the *vegan* package. Prior to these analyses, testing of multi-collinearity within the matrices (using calculation of variance inflation factors) and a forward selection of explanatory variables had been performed using the *forward.sel* function in the *packfor* package (Dray et al. 2013).

Multivariate regression tree (MRT) analysis was used to identify which measured environmental variables partition the best the survival of planted maple seedlings. This method also allowed identifying if survival patterns between forest types are representative of specific variations in selected environmental variables. Analysis was respectively used on seedlings planted in soil and in pots using the *mvpart* function of the *mvpart* package.

All coefficients of determination ($R^2$) that were obtained from the aforementioned analyses, and which were reported in this study as a means of explaining variation in the data set, are the adjusted $R^2$ values, hereafter denoted as $R^2_a$. The $R^2_a$ is the unbiased form of the coefficient that takes into account the number of input variables in the model. It is required when performing variation partitioning (Peres-Neto et al. 2006). When not provided directly by the analysis or function, $R^2_a$ was calculated with the *RsquareAdj* function in the *vegan* package.

## 2.4 Results

### 2.4.1 Stand characteristics

Basal area of conifer-dominated stands was significantly higher than mixed hardwood-conifer stands and maple-beech stands (Table 2.1). As an attempt to characterize light availability in the understory of each forest type, we analyzed the percentage of canopy openness within each plot. Results revealed that maple-beech stands had a significantly lower canopy openness compared to the other forest types studied (Figure 2.1). Moreover, canopy openness was significantly lower in maple-beech stands without maple seedling regeneration than maple-beech stands with the presence of maple seedlings.

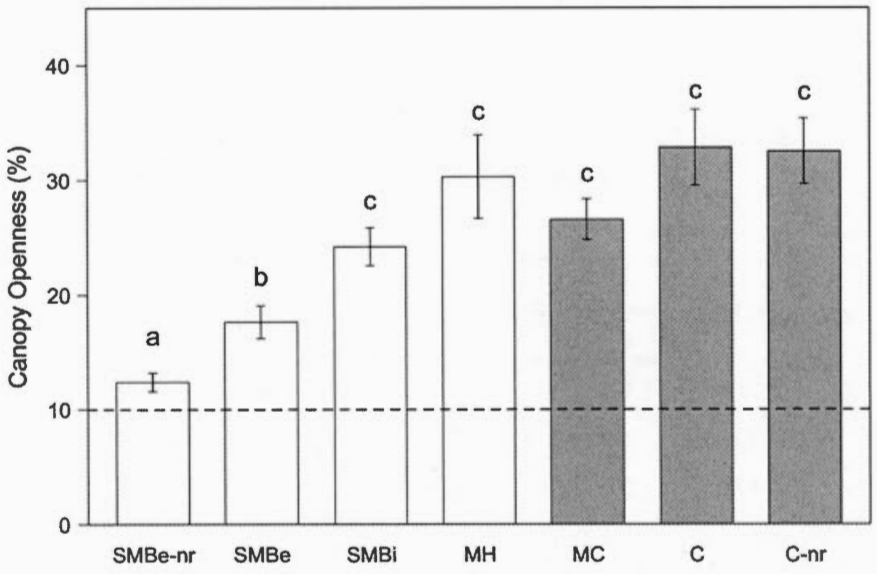


**Figure 2.1** Canopy openness of the various forest types studied, which is used as a proxy for understory light availability. Grey bars indicate conifer-dominated stands. Means are presented with standard errors. Different letters indicate a statistically significant difference at $P < 0.05$. SMBe is maple-beech stands, SMBi is maple-birch stands, MH is mixed hardwood-conifer stands with dominance of hardwoods, MC is mixed hardwood-conifer stands with dominance of conifers, C is conifer-dominated stands, and nr is no maple regeneration. The dotted line indicates the threshold under which maple cannot regenerate (Yawney 1976).

## 2.4.2 Foliage

Foliar nutrient levels of naturally regenerated maple seedlings varied significantly between forest types (Table 2.2). Seedlings under hardwood and mixed hardwood-conifer stands had higher foliar Ca and Mg levels than under conifer-dominated stands. Foliar N levels were significantly higher in mixed hardwood-conifer stands dominated by conifers than those dominated by hardwoods. Similarly, seedlings under mixed hardwood-conifer stands dominated by conifers had

significantly higher foliar P levels than in any other forest type studied, whereas foliar P levels under maple-beech stands were significantly lower than in other forest types.

**Table 2.2** Foliar nutrient levels of sugar maple seedlings in the various forest types studied.

| Forest type | Foliar nutrients (mg/g) | | | | |
|---|---|---|---|---|---|
| | N | P | K | Ca | Mg |
| SMBe | 17.45 (±0.59) ab | 0.98 (±0.05) c | 5.80 (±0.87) | 9.22 (±1.03) a | 2.03 (±0.25) a |
| SMBi | 18.54 (±1.20) ab | 1.14 (±0.08) b | 5.87 (±0.66) | 8.89 (±0.46) a | 2.05 (±0.26) a |
| MH | 17.00 (±0.91) b | 1.08 (±0.05) b | 6.55 (±0.67) | 8.44 (±0.72) ab | 1.86 (±0.20) ab |
| MC | 19.03 (±1.28) a | 1.29 (±0.08) a | 6.62 (±1.11) | 9.11 (±0.79) a | 2.08 (±0.24) a |
| C | 18.96 (±1.43) ab | 1.09 (±0.07) b | 6.45 (±0.65) | 7.86 (±0.75) b | 1.67 (±0.21) b |

Means are presented with standard errors. Different letters indicate a statistically significant difference at $P < 0.1$. Percent contributions by individual species not tested. SMBe is maple-beech stands, SMBi is maple-birch stands, MH is mixed hardwood-conifer stands with dominance of hardwoods, MC is mixed hardwood-conifer stands with dominance of conifers and C is conifer-dominated stands.

Foliage of maple seedlings under maple-beech stands had significantly less total chlorophyll, chlorophyll *a* and carotenoids than maple foliage under most other forest types (Table 2.3). Chlorophyll *b* of maple foliage was also significantly lower under maple-beech stands than under the mixed hardwood-conifer stands dominated by conifers and the conifer-dominated stands. Chlorophyll (*a*, *b* and total) and carotenoid levels were highly correlated with foliar N and P levels ($r > 0.64$, $P < 0.01$), and negatively correlated with the proxy of intensity of herbivory ($r < -0.60$, $P < 0.01$).

Leaf scans used in an attempt to characterize the intensity of herbivory indicated a significantly higher leaf damage on maple seedlings under maple-beech stands than on maple seedlings under other forest types (Figure 2.2).

**Table 2.3** Foliar chlorophyll (*a*, *b* and total) and total carotenoids levels of sugar maple seedling in the various forest types studied.

| Forest type | Leaf pigments (mg/g of Fresh Matter) | | | |
|---|---|---|---|---|
| | Chlorophyll | | | Carotenoids |
| | *a* | *b* | Total | Total |
| SMBe | 2.40 (±0.16) a | 1.47 (±0.11) a | 3.87 (±0.27) a | 0.52 (±0.03) a |
| SMBi | 2.96 (±0.47) b | 1.68 (±0.23) ab | 4.64 (±0.70) ab | 0.63 (±0.09) b |
| MH | 2.85 (±0.23) b | 1.66 (±0.14) ab | 4.51 (±0.36) b | 0.62 (±0.04) b |
| MC | 3.45 (±0.38) b | 1.83 (±0.20) b | 5.28 (±0.55) b | 0.74 (±0.07) b |
| C | 3.41 (±0.38) b | 1.88 (±0.14) b | 5.29 (±0.49) b | 0.74 (±0.08) b |

Means are presented with standard errors. Different letters indicate a statistically significant difference at $P < 0.05$. Percent contributions by individual species not tested SMBe is maple-beech stands, SMBi is maple-birch stands, MH is mixed hardwood-conifer stands with dominance of hardwoods, MC is mixed hardwood-conifer stands with dominance of conifers and C is conifer-dominated stands.

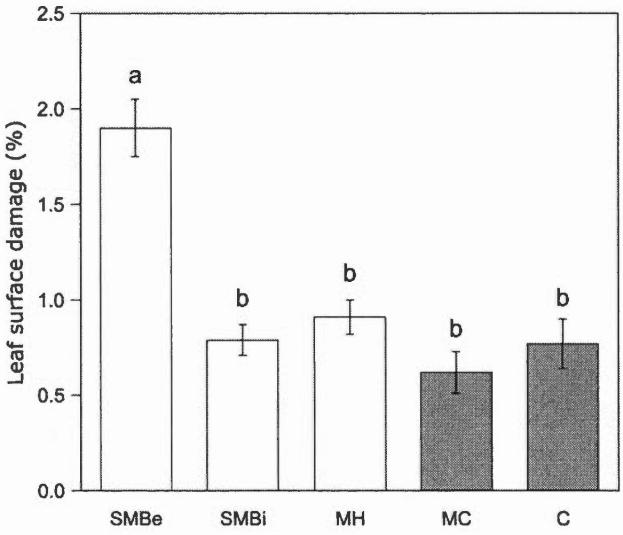


**Figure 2.2** Leaf surface damage of sugar maple seedlings in the various forest types studied as recorded using the surface of holes that were created by herbivores relative to the total leaf area (%). Grey bars indicate conifer-dominated stands. Means are presented with standard errors. Different letters indicate a statistically significant difference at $P < 0.05$. SMBe is maple-beech stands, SMBi is maple-birch stands, MH is mixed hardwood-conifer stands with dominance of hardwoods, MC is mixed hardwood-conifer stands with dominance of conifers and C is conifer-dominated stands.

### 2.4.3 Survival experiment of planted maple seedlings

After 456 days, 105 out of 218 planted seedlings had survived (47%). Maple seedlings that were planted in the natural soil had a significantly lower survival under the maple-beech stands than those under both types of mixed hardwood-conifer stands (Table 2.4). Similar results were also found for maple seedlings planted in fertilized pots. No significant differences were found in height growth between forest types, whether they were planted in the natural soil or in the pots. However, comparisons in height growth indicate that maple seedlings planted in pots grew at a significantly higher rate than seedlings planted in the natural soil (Table 2.4).

**Table 2.4** Survival rates and relative height growth of the sugar maple seedlings planted in the natural soil and pots under the various forest types studied as measured at the end of the trial (456 days).

| Forest type | n | | Survival rate (%) | | Height growth (%) | |
|---|---|---|---|---|---|---|
| | Soil | Pot | Soil | Pot | Soil | Pot |
| SMBe-nr | 1 | 0 | 5 b | 0 c | 3.5 | - |
| SMBe | 3 | 0 | 15 (±8.19) b | 0 c | 9.9 (±2.8) | - |
| SMBi | 7 | 3 | 35 (±10.9) ab | 25 (±13.1) bc | 19.9 (±2.4) | 36.8 (±17.5) |
| MH | 20 | 8 | 100 a | 66.7 (±14.2) a | 22.5 (±3.4) | 44.5 (±12.2) |
| MC | 20 | 11 | 100 a | 91.7 (±8.3) a | 20.4 (±2.5) | 47.2 (±12.6) |
| C | 11 | 7 | 55 (±11.4) ab | 58.3 (±14.9) ab | 20.7 (±2.2) | 37.1 (±8.9) |
| C-nr | 9 | 5 | 45 (±13.3) ab | 41.7 (±17.6) abc | 23.7 (±4.0) | 44.7 (±13.7) |
| Planting comparison | | | | | | |
| *P*-value | | | 0.371 | | <0.001 | |

Means are presented with standard errors when available. Different letters indicate a statistically significant difference at $P < 0.05$. SMBe is maple-beech stands, SMBi is maple-birch stands, MH is mixed hardwood-conifer stands with dominance of hardwoods, MC is mixed hardwood-conifer stands with dominance of conifers, C is conifer-dominated stands, and nr is no maple regeneration.

### 2.4.4 Soils

Linear discriminant analysis showed a clear partitioning of soil properties between hardwood stands, including mixed hardwood-conifer stands dominated by hardwoods, and conifer-dominated stands, including mixed hardwood-conifer stands dominated by conifers (Figure 2.3). Both types of mixed hardwood-conifer stands tended, however, to separate from either hardwood or conifer-dominated stands along the second axis. Also, a posteriori analysis indicated an overall correct classification of each measurement to the designed class of forest types. The discrimination appears to be mainly driven by soil temperature, VWC, phenols and forest floor pH.

Particle size distribution of the B horizons is quite homogeneous across forest types (Table 2.5). It is characterized by low clay content (2.20 to 3.92%), with silt and sand averaging 40% and 57%, respectively. The conifer-dominated stands with no maple seedling regeneration have slightly higher silt and clay and lower sand than other forest types. Soil VWC and temperature significantly decreased from hardwoods to conifer-dominated stands (Table 2.5).

Average forest floor pH values ranged from 4.03 to 4.55, with conifer-dominated and mixed hardwood-conifer stands dominated by conifers being the most acidic, followed by mixed hardwood-conifer stands dominated by hardwoods and hardwood stands (Table 2.5). pH values in the B horizon ranged from 4.55 to 5.16 and the trend in acidity with conifers is not as obvious, although the conifer-dominated stands without maple seedling regeneration are significantly more acidic than all other forest types.

Soil solution ionic activity differed substantially between forest types (Table 2.6) and is related to forest floor pH ($P < 0.05$, multivariate relationship). Soil solution $NO_3^-$ and $NH_4^+$ (hereafter referred to as N), Ca, Mg and Al activities were higher in hardwood stands than in mixed hardwood-conifer and conifer-dominated stands.

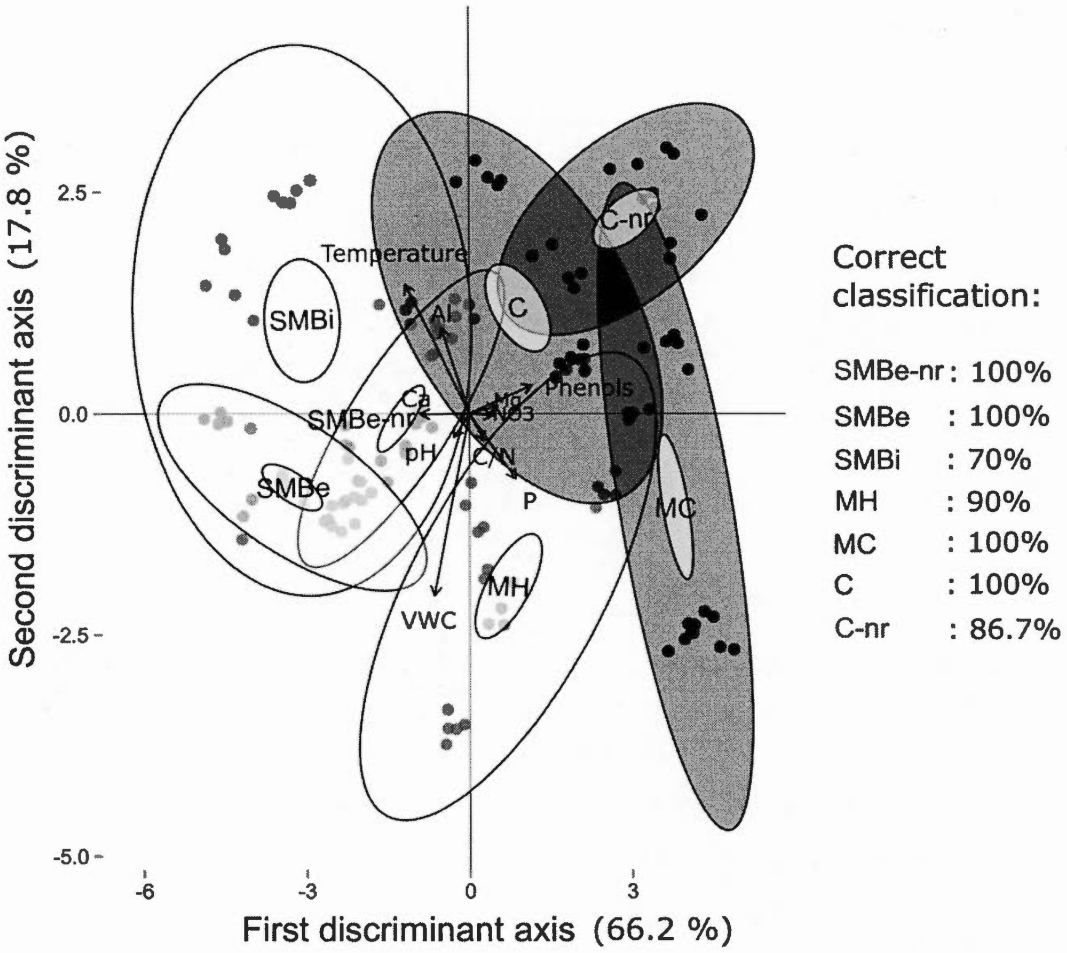


**Figure 2.3** Linear discriminant analysis of soil chemical properties (i.e. pH, soil solution ionic activity and phenolic compounds), temperature and volumetric water content (VWC) by forest type. Grey ellipses indicate conifer-dominated stands. The ellipses surround 95% of the theoretical inner-group dispersion. SMBe is maple-beech stands, SMBi is maple-birch stands, MH is mixed hardwood-conifer stands with dominance of hardwoods, MC is mixed hardwood-conifer stands with dominance of conifers, C is conifer-dominated stands, and nr is no maple regeneration.

**Table 2.5** Physical and chemical properties of the forest floors and B horizons in the various forest types studied.

| Forest type | FH horizon | | | | | |
|---|---|---|---|---|---|---|
| | pH | | VWC | | Temperature* | |
| | | | % | | °C | |
| SMBe-nr | 4.50 | (±0.16) a | 20.35 | (±0.37) a | 7.12 | (±0.04) a |
| SMBe | 4.55 | (±0.20) ab | 20.90 | (±0.82) a | 7.10 | (±0.08) ab |
| SMBi | 4.47 | (±0.10) ab | 20.32 | (±1.20) a | 7.15 | (±0.12) ab |
| MH | 4.26 | (±0.09) abc | 16.18 | (±1.30) ab | 7.14 | (±0.10) ab |
| MC | 4.12 | (±0.08) c | 12.30 | (±1.10) bc | 6.66 | (±0.16) abc |
| C | 4.03 | (±0.07) c | 13.80 | (±0.39) bc | 6.69 | (±0.12) bc |
| C-nr | 4.11 | (±0.12) bc | 11.03 | (±0.58) c | 6.63 | (±0.06) c |

| Forest type | B horizon | | | | | |
|---|---|---|---|---|---|---|
| | pH | | Clay | | Silt | Sand |
| | | | % | | % | % |
| SMBe-nr | 4.81 | (±0.06) a | 3.13 | (±0.44) | 37.98 (±4.76) | 58.67 (±5.03) |
| SMBe | 4.84 | (±0.08) a | 3.17 | (±0.78) | 45.22 (±6.97) | 51.61 (±7.73) |
| SMBi | 4.98 | (±0.10) a | 2.20 | (±0.41) | 38.44 (±1.60) | 59.37 (±1.96) |
| MH | 5.05 | (±0.08) a | 2.93 | (±0.34) | 41.06 (±2.21) | 56.01 (±2.51) |
| MC | 5.16 | (±0.12) a | 2.80 | (±0.35) | 33.55 (±3.41) | 63.66 (±3.75) |
| C | 4.90 | (±0.17) a | 2.21 | (±0.44) | 35.37 (±1.67) | 62.43 (±2.07) |
| C-nr | 4.55 | (±0.20) b | 3.92 | (±0.14) | 48.16 (±2.49) | 47.91 (±2.55) |

*measured under the forest floor, at the interface with the mineral soil, during the growing season (May to October of 2013). VWC is volumetric water content. Means are presented with standard errors. Different letters indicate a statistically significant difference at $P < 0.05$. Percent contributions by individual species not tested. SMBe is maple-beech stands, SMBi is maple-birch stands, MH is mixed hardwood-conifer stands with dominance of hardwoods, MC is mixed hardwood-conifer stands with dominance of conifers, C is conifer-dominated stands, and nr is no maple regeneration.

**Table 2.6** Soil solution ionic activity in the various forest types studied as recorded by the PRS$^{TM}$ probes.

| Forest type | Soil solution ionic activities (µg/10cm/2month) | | | | |
|---|---|---|---|---|---|
| | N | P | K | Ca | Mg |
| SMBe-nr | 33.3 (±17.6) | 1.99 (±0.81) | 34.0 (±6.88) | 978 (±119) | 154 (±22.8) |
| SMBe | 35.2 (±19.9) | 0.97 (±0.27) | 45.2 (±14.8) | 974 (±127) | 153 (±26.2) |
| SMBi | 58.7 (±35.8) | 1.85 (±0.70) | 72.7 (±11.3) | 787 (±38.4) | 147 (±9.01) |
| MH | 6.00 (±1.04) | 1.93 (±0.69) | 72.0 (±7.83) | 591 (±100) | 115 (±20.6) |
| MC | 3.50 (±0.43) | 1.15 (±0.30) | 84.0 (±7.41) | 389 (±22.7) | 84.0 (±17.2) |
| C | 3.67 (±0.40) | 3.77 (±2.25) | 63.7 (±15.9) | 720 (±100) | 121 (±16.0) |
| C-nr | 4.00 (±0.51) | 1.78 (±0.29) | 72.0 (±0.29) | 569 (±62.3) | 104 (±18.5) |
| Forest type | Soil solution ionic activities (µg/10cm/2month) | | | | |
| | Al | Mn | Fe | | |
| SMBe-nr | 43.3 (±4.92) | 7.80 (±2.78) | 6.87 (±0.85) | | |
| SMBe | 47.9 (±8.27) | 8.87 (±0.87) | 5.00 (±1.72) | | |
| SMBi | 97.3 (±27.6) | 13.1 (±4.75) | 7.07 (±1.47) | | |
| MH | 38.7 (±3.73) | 5.83 (±1.51) | 6.55 (±0.93) | | |
| MC | 31.5 (±4.21) | 7.13 (±2.38) | 5.13 (±1.09) | | |
| C | 39.2 (±4.83) | 8.27 (±1.60) | 6.52 (±1.36) | | |
| C-nr | 36.5 (±3.68) | 11.3 (±5.33) | 3.15 (±0.50) | | |

*includes $NO_3$ and $NH_4$. Means are presented with standard errors. Different letters indicate a statistically significant difference at $P < 0.05$. Percent contributions by individual species not tested. SMBe is maple-beech stands, SMBi is maple-birch stands, MH is mixed hardwood-conifer stands with dominance of hardwoods, MC is mixed hardwood-conifer stands with dominance of conifers, C is conifer-dominated stands, and nr is no maple regeneration.

Soils of the maple-beech and conifer-dominated stands without maple seedling regeneration had significantly higher levels of phenols compared to other hardwood stands, including maple-beech stands with maple seedling regeneration and mixed hardwood-conifer stands dominated by hardwoods (Figure 2.4). Conifer-dominated stands with maple seedling regeneration, including mixed hardwood-conifer stands dominated by conifers, showed intermediate levels of phenols in the soil, but these were not significantly different from any other forest types studied.

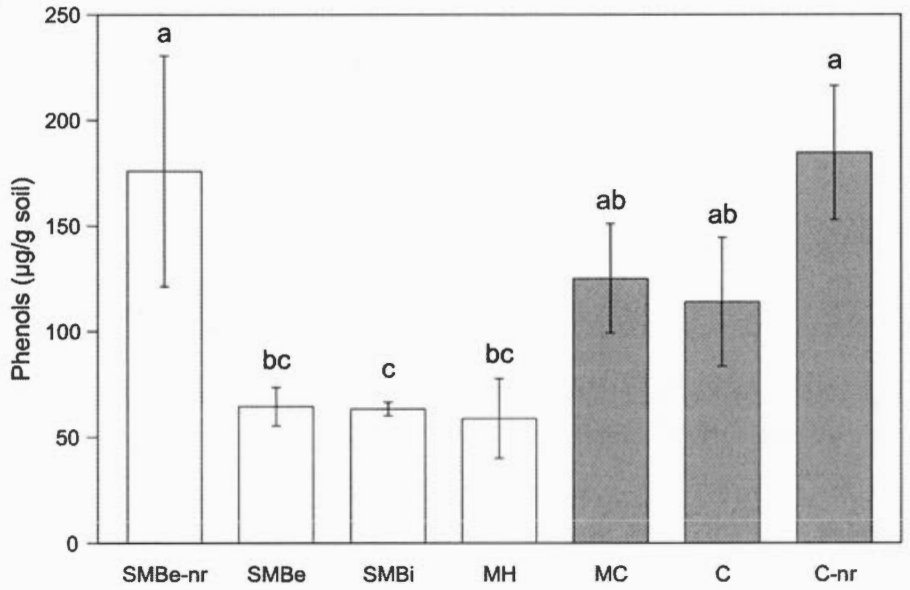


**Figure 2.4** Levels of phenolic compounds measured under the forest floor of the various forest types studied as recorded by the resin bags. Grey bars indicate conifer-dominated stands. Means are presented with standard errors. Different letters indicate a statistically significant difference at $P < 0.05$. SMBe is maple-beech stands, SMBi is maple-birch stands, MH is mixed hardwood-conifer stands with dominance of hardwoods, MC is mixed hardwood-conifer stands with dominance of conifers, C is conifer-dominated stands, and nr is no maple regeneration.

Calcium and P levels in the 0.1 M HCl leachates of the B horizon showed a general decrease with decreasing forest floor pH and increasing proportion of conifers in the following order: maple-birch stands ≥ maple-beech stands ≥ mixed hardwood-conifer stands ≥ conifer-dominated stands (Figure 2.5A, B). Particularly, significantly higher Ca and P levels were found in the higher pH soils of the maple-beech and maple-birch stands compared to the more acidic soils of the conifer-dominated stands, including mixed hardwood-conifer stands dominated by conifers in the case of P. The mean molar Ca/P ratios in the various forest types were above 4 (Figure 2.5C). The mean ratios were similar between most forest types (4 to 7), except for mixed hardwood-conifer stands dominated by conifers which had a mean molar Ca/P ratio of 11 but a large standard error (Figure 2.5C).

### 2.4.5 Models of foliar nutrients and seedling survival

Using redundancy analysis, and after removing collinearities between variables, it was found that the most robust model explaining variation in foliar nutrients was composed of forest floor pH and volumetric water content (VWC). This model explained as much as 52% of the variation in foliar nutrients of maple seedlings ($P < 0.001$). This is a more robust model than expected considering that maple seedlings originated from a natural system with uncontrolled growing conditions, hence increasing variability and uncertainty toward explaining factors. Variation partitioning was also conducted to quantify the respective contribution of each environmental variables selected in the model. Forest floor pH explained 39% of the total variation in foliar nutrients and soil VWC explained 13% of the total variation.

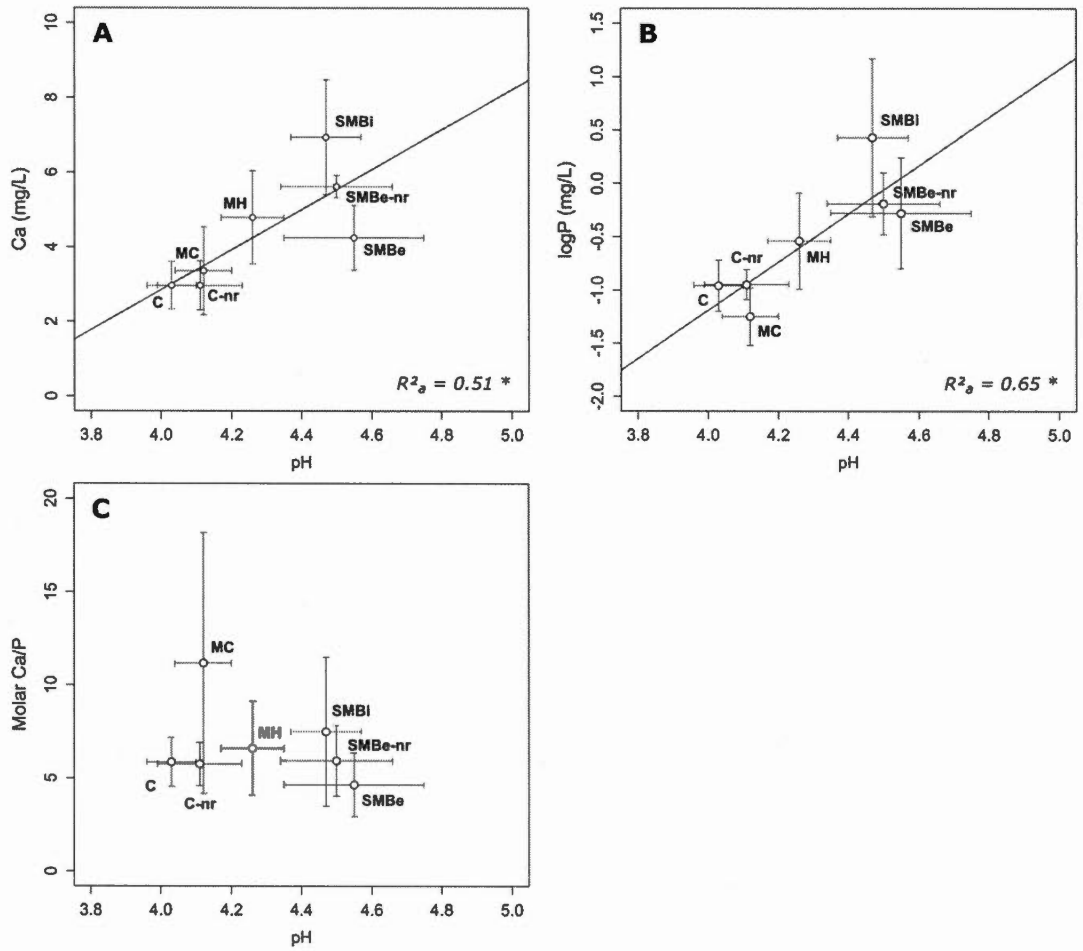


**Figure 2.5** Relationships between pH and (A) Ca levels, (B) P levels, and (C) molar Ca/P ratios in the 0.1 M HCl B horizon leachates of the various forest types studied. Means are presented with standard errors. SMBe is maple-beech stands, SMBi is maple-birch stands, MH is mixed hardwood-conifer stands with dominance of hardwoods, MC is mixed hardwood-conifer stands with dominance of conifers, C is conifer-dominated stands, and nr is no maple regeneration. Significance designated as * $P < 0.05$

Similarly to foliar nutrients, we attempted to explain variation in survival rates using environmental variables as explanatory variables. The model that best explained the survival rates included canopy openness, Al ionic activity in the soil solution (as measured by PRS$^{TM}$ probes) and tree basal area ($R^2_a = 0.56$, $P < 0.001$). Results of the MRT analysis suggested that only one measured environmental variable, i.e. canopy openness, partition the best the survival of maple seedlings, independently of planting condition ($R^2_a = 0.54$) (Figure 2.6). In this experiment, a critical threshold was determined at 22% of canopy openness under which planted maple seedlings have not survived. MRT analysis on height growth of planted seedling did not return any results. However, we found that growth was significantly positively correlated to canopy openness ($r = 0.20$, $P < 0.05$), independently of planting conditions.

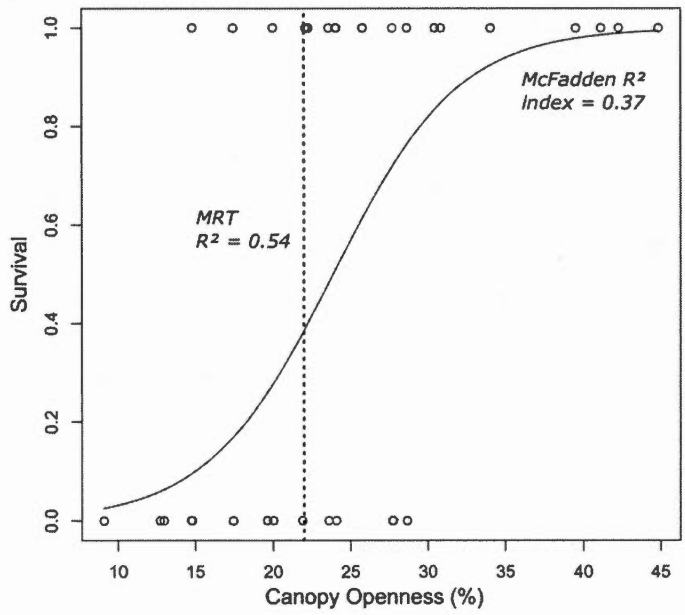


**Figure 2.6** Logistic regression of planted maple seedlings survival along canopy openness of forest types. The dotted line is the result of the multivariate regression tree (MRT) analysis partitioning the probability of seedlings survival.

## 2.5 Discussion

### 2.5.1 Maple regeneration under maple-beech stands

Our first hypothesis that regeneration failure of maple seedlings under the maple-beech stands may be related to low light availability is supported by our results (Figures 2.1 and 2.6). Light levels under maple-beech stands with no maple regeneration were significantly lower than that found in other forest types. Beech has greater crown projection and productivity than maple under closed canopy conditions (Takahashi and Lechowicz 2008). A light availability threshold was proposed to favour beech over maple below 30% of shade (Nolet et al. 2008a), whereas a significant decline in the development of maple seedlings was observed under 90% of shade (Yawney 1976). In our case, 12.4% of canopy openness measured in maple-beech stands without maple regeneration (compared to 17.6% of canopy openness under maple-beech stands with maple regeneration, Figure 2.1) is a likely factor supressing maple seedling establishment and/or survival. The results of the survival experiment are also consistent with the idea that the presence of beech is adversely affecting maple seedling survival (Table 2.4 and Figure 2.6). Because survival under maple-beech stands was severely impeded for maple seedlings planted in both the natural soil (nutrient-poor) and pots (nutrient-rich soil), it is likely that factors independent of soil properties, e.g. light availability, are mainly involved.

Additionally, we monitored high levels of phenolic compounds under maple-beech stands along with greater leaf damage of maple seedlings (Figure 2.2 and 2.4). High levels of phenols can effectively repress seed germination and seedling development by further exacerbating seedling nutrition and fitness (Hane et al. 2003). Plant diversity and species richness beneath allopathic trees is classically found to be lower compared to adjacent plots without the allelopathic cover plant (Souto et al. 1995). While beech is known to produce large amounts of secondary compounds, including polyphenolics (Coldwell and DeLong 1950, Smith 1976, Hane et al. 2003),

seedling and sapling diversity and density under maple-beech stands with no regeneration of maple in St. Hippolyte were remarkably lower than under other forest types (A. Collin, personal observation). Cale et al. (2013) also found that beech sapling density explained 38% of groundcover plant species diversity, but they did not separate the effects of allelopathy from shading. Since direct effect of allelopathy by beech on maple survival was not isolated in our experiment, great care is needed while inferring a potential causation. In regard to the soil variables measured (Tables 2.5 and 2.6, Figure 2.4), only phenol levels differed between maple-birch and maple-beech stands, thus suggesting a greater effect of phenols compared to other soil properties. However, as no significant differences were found with conifer covers under which maple is able to regenerate indicate that only light availability may control maple seedling survival under beech. Nevertheless, a combination of shading and phytotoxic effects of beech negatively impacting maple regeneration by supressing seedling development and in turn survival rates cannot be entirely excluded, as demonstrated by Hane (2003) and Hane et al. (2003). .

Of other superimposed effects that may affect maple seedling survival, herbivory pressure and presence of pathogens are possible factors (Cleavitt et al., 2014). While pathogens were not examined or observed in this study, greater leaf damage of maple seedlings under maple-beech stands is an indication of higher herbivory pressure on maple under that particular forest type (Figure 2.2). Animals such as deer are known to prefer maple leaves over beech leaves (Marquis and Brenneman 1981, Côté et al. 2004, Long et al. 2007). However, our proxy only reflects the smallest impacts of defoliation since we were able to record only the smallest visible leaf damage presumably done by insects. It cannot be used to assess browsing intensity by animals such as deer because leaves are likely consumed entirely under such pressure. Nevertheless, since the proxy of herbivory pressure was highly negatively correlated with chlorophyll and carotenoids (Table 2.3), we suggest

that this may negatively affects plant competitiveness by impacting photosynthetic rates.

### 2.5.2 Maple regeneration under conifer-dominated stands

The results of the survival experiment did not support our hypothesis that maple seedling survival is negatively impacted by lower soil pH and nutrient availability under conifer canopies. However, soil conditions and foliar nutrients of maple seedlings supported that the absence of regeneration under some conifer-dominated stands in St. Hippolyte could be related to specific soil conditions (e.g. pH, humidity, temperature) and low soil nutrient availability that impede maple regeneration and early seedling growth. Three explanations are provided here.

First, conifer-dominated stands with no maple regeneration were found to be dominated by eastern hemlock compared to other conifer-dominated stands (Table 2.1). Eastern hemlock is a species known to exclude maple by adversely influencing maple germination and seedling regeneration due to unsuitable forest floor conditions (Frelich et al. 1993). Presence of hemlock in some stands in St. Hippolyte may have favoured the creation of a specific type of forest floor that is not optimal for regeneration success of maple. The thick, acidic and drier forest floor under the conifer-dominated stands also showed lower soil nutrient availability (including N, Ca and Mg) than forest floors produced by other forest types (Table 2.6). Immobilization of nutrients is typical of recalcitrant forest floors produced mainly from coniferous litters (Finzi et al. 1998, Zak et al. 1999). In St. Hippolyte, this led mainly to lower foliar Ca and Mg levels of maple seedlings, suggesting that fitness has been negatively impacted by conifer dominance (Tables 2.2 and 2.5). Maple is known to be very sensitive to Ca and Mg availability for its survival and growth (Houle et al. 2007, St. Clair et al. 2008, Long et al. 2009). Declining maple stands were generally related to low foliar Ca, Mg and K levels (Côté and Camire 1995,

Ouimet et al. 2006, Duchesne and Ouimet 2009) and liming generally enhanced maple health (Moore and Ouimet 2006, Schaberg et al. 2006, Moore et al. 2014). Collin et al. (2016) showed a similar negative effect of conifer dominance on foliar Ca and Mg nutrition of maple seedlings under other climates and soil types in Quebec. Also, while pH of the mineral soil was relatively similar between forest types, conifer-dominated stands without maple regeneration distinguished themselves by having a significantly more acidic mineral soil (Table 2.5).

Secondly, soils under conifer-dominated stands without maple regeneration had similar levels of phenolic compounds than soils under maple-beech stands without maple regeneration (Figure 2.4). Allelopathic effects appears to occur more intensely in poor soils where slow organic matter decomposition is accompanied by the characteristic production of phenolic compounds which can inhibit nitrification and thus effectively decrease nutrient availability (Hättenschwiler and Vitousek 2000, DeLuca et al. 2002). Hence, the greater soil acidity budget in this forest type is likely promoting greater production of phenols (Blum 2006). As speculated previously for maple-beech stands with no maple regeneration, the high levels of phenols in some conifer-dominated stands may effectively repress seed germination and seedling development by further exacerbating seedling nutrition and fitness (Hane et al. 2003).

Finally, the absence of maple regeneration under some conifer-dominated stands could be explained by additional factors related to soil microclimate and tree density. To germinate, maple seeds require moist stratification at temperatures slightly above freezing and below 10°C for 35 to 90 days (Yawney and Carl Jr 1968, Godman et al. 1990). Therefore, lower mean annual soil temperature and VWC during the growing season under conifer-dominated stands (Table 2.5) is not uncommon for various reasons [e.g. greater interception of light (Penn et al. 2012) and of rainfall (Lovett et al. 1996, Barbier et al. 2009) by the persistent and dense conifer canopies]. This has the potential to further (negatively) affect maple seed

germination and seedling survival at early stages of growth. Seedlings are likely more sensitive to temperature and drought than adult plants because they have smaller and shallower root systems that cannot as easily avoid high soil surface temperatures during hot summer days and water stress by accessing deeper soil water reserves (Niinemets 2010, Fisichelli et al. 2014). Maple seedlings are particularly susceptible to water stress (Hett 1971, Godman et al. 1990). Moreover, conifer-dominated stands have higher basal area (Table 2.1). This may reflect a higher competition for soil resources. However, we can also consider that, for those stands, only very few maple trees were present in the surroundings, thus highly reducing seed availability for colonization. Higher tree density in conifer-dominated stands can also be a limiting factor for seed dispersal compared to other forest types by acting as a physical barrier.

Results from the survival experiment did not provide evidence toward a factor explaining regeneration failure of natural maple seedlings under conifer-dominated stands. Higher height growth rates of maple seedlings planted in pots compared to those planted in the natural soil (Table 2.4) confirms that mixing the local mineral soil with a premium potting mix containing peat, perlite, limestone and vesicular-arbuscular mycorrhizae in combination with fertilization provided nutrients for a more optimal growth than the natural soil. However, because no clear statistical difference was found in height growth of the seedlings that had survived in the natural soil under the various forest types, it again appears that soil nutrient availability is a complementary factor explaining survival. Seedlings were grown in nursery for 2 years under optimal nutrient availability prior to being planted. Over 1.5 years of experimenting, we can therefore assume that nutrient reserves were sufficient for survival rates of seedlings planted in the natural soil, under lower nutrient availability, to be similar to those planted in pots, under higher nutrient availability (Oliet et al. 2013).

### 2.5.3 Soil mineral weathering by specific conifer species

Assuming that the parent material in St. Hippolyte was relatively homogeneous in terms of bulk chemical composition and mineralogy at the time it was deposited by the continental ice sheets, the results from the sequential leaching of the B horizon samples suggest that the most easily weathered minerals have been leached from the soil at a faster rate under stands with the presence of conifers, i.e. mixed hardwood-conifer and conifer-dominated stands, compared to hardwood stands. This is indicated by lower levels of structural Ca and P in minerals as simulated by HCl leaches of mixed hardwood-conifer and conifer-dominated stands mineral soils, which is related to greater forest floor acidity (Figure 2.5A, B). Considering previous work on soil mineralogy at the St. Hippolyte study site (Bélanger et al. 2012), the results can be interpreted by a lower abundance of calcite, apatite and epidote in the soils of the mixed hardwood-conifer and conifer-dominated stands because of the acidity that they have produced from their litters and other sources (Finzi et al. 1998, Augusto et al. 2000), thus augmenting dissolution rates. Weathering rates were suggested to increase under conifer species such as pines, spruces and firs because of their capacity to acidify soils (see review by Augusto et al. (2000)). In the long-term, higher dissolution rates of easily weathered minerals and greater depletion of soil non-exchangeable base cation reserves under conifer-dominated stands in St. Hippolyte appears to have led to a decrease in foliar Ca and Mg levels of maple seedlings (Table 2.2). This decrease in Ca and Mg seems to apply for the overall system of conifer-dominated stands as Ca and Mg activities in the soil solution are also low under this forest type (Table 2.6).

Mixed hardwood-conifer stands dominated by conifers generally showed the highest foliar P levels among the forest types studied (Table 2.2). This result was surprising, given that the activity of the soil solution of most nutrient ions tended to be among the lowest of all the forest types studied (Table 2.6). The fact that molar

Ca/P ratios under all forest types were above 4 (Figure 2.5C) suggests that Ca-rich minerals such as epidote and perhaps calcite (aluminium-iron sorosilicate and calcium carbonate minerals, respectively) are contributing more Ca and less P compared to apatite (pure apatite ($CaPO_4$) has a stoichiometry fixed at a molar Ca/P ratio of 1.66) into the leachates (Bélanger et al. 2012). The Ca/P ratios are also generally similar between forest types, which suggest that the minerals have been congruently leached, despite variations in conifer abundance (Figure 2.5C). Hence, weathering appears to have occurred at a faster rate where conifers were present, but they did not trigger a preferential dissolution within these easily weathered minerals.

The mixed hardwood-conifer stands dominated by conifers may be one exception to that rule. The higher molar Ca/P ratios under this forest type (mean of 11, but with a large variation) could indicate a greater depletion of apatite over epidote and calcite in the long term. Using Sr isotope ratios, balsam fir and red spruce are the ectomycorrhizal tree species that were shown to largely utilize apatite-derived calcium (Blum et al. 2002). It was suggested that ectomycorrhizal fungi produce low molecular weight organic acids that dissolve apatite. In turn, associated roots directly absorb the ions from the crystal lattice of the mineral, thus bypassing the soil solution and exchangeable soil pool. *Pinus* spp. were also shown to have ectomycorrhizal associations with roots that accelerate weathering of minerals and podzolic soil formation (Van Breemen et al. 2000, Hoffland et al. 2004). On the one hand, the conifers in the mixed hardwood-conifer stands dominated by conifers are mostly ectomycorrhizal species, i.e balsam fir, spruces and eastern white pine (Table 2.1) (Frank 1990, Wendel and Smith 1990). On the other hand, the conifer-dominated stands have a large proportion of white cedar and eastern hemlock. White cedar is an arbuscular mycorrhizal species, whereas eastern hemlock is both an arbuscular and ectomycorhizal species (Godman and Lancaster 1990, Johnston 1990). While recent evidence suggest that arbuscular mycorrhizal fungi can also dissolve minerals (Arocena et al. 2012, Koele et al. 2014), they facilitate slower weathering rates than

ectomycorrhizal fungi (Quirk et al. 2012). It is therefore possible that the ectomycorrhizal associations with conifer roots under mixed hardwood-conifer stands dominated by conifers have degraded the most easily weathered minerals, notably apatite, at a faster rate and to specific levels that favored P nutrition of maple seedlings and perhaps Ca and Mg nutrition as well (as shown by relatively high foliar levels compared to other forest types, Table 2.2). Since there was low activity of most nutrient ions in the soil solution under hardwood-conifer stands dominated by conifers, including $PO_4$, Ca and Mg, we suspect that arbuscular mycorrhizal fungi and perhaps other soil organisms, e.g. saprotrophic fungi and rhizosphere bacteria (Clark and Zeto 2000, Koele et al. 2014), have direct access to P, Ca and Mg from the degraded minerals to satisfy at least part of P, Ca and Mg maple seedling needs. Other candidate minerals for such a mechanism of maple seedling nutrition are epidote for Ca and hornblende for Mg (Holmden and Bélanger 2010, Bélanger et al. 2012). As a whole, the conifer tree species that co-exist with maple may therefore be important for determining long-term nutrition, fitness and survival of maple seedlings.

## 2.6 Conclusion

Results from this study indicate that regeneration and foliar nutrition of sugar maple seedlings are strongly influenced by tree species composition. First, the presence of beech can negatively affect the resilience of maple by impacting its regeneration success. This effect is the consequence of low light availability. The cumulative effects of high levels of soil phenols as well as of preferential herbivory pressure are likely superimposed factors explaining maple seedling survival and growth failures. In addition, results support the idea that coniferous species have a negative effect on foliar nutrition of maple seedlings. This effect is governed by the recalcitrant (thick), acidic and drier forest floor under conifer-dominated stands with

low forest floor nutrient availability, which leads to poor foliar Ca and Mg nutrition. Calcium and Mg are important for the health and vigour of maples in eastern North America. The absence of regeneration under some conifer-dominated stands in St. Hippolyte could also be related to the long term acidification of the mineral soil, low soil temperature and moisture, and high soil phenol levels. The data also suggest an accelerated dissolution of easily weathered minerals under conifer-dominated stands. However, the weathering of minerals by ectomycorrhizal roots of some conifer tree species may have occurred in a way that favoured foliar P, Ca and Mg nutrition of maple seedlings. This suggest that, depending on soil properties, maple seedling survival and fitness as well as its potential to migrate may be facilitated by specific conifer tree species, e.g. spruce, fir and pine, and hindered by others, cedar and hemlock.

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CHAPITRE III

# CONTRASTING NUTRITIONAL ACCLIMATION OF SUGAR MAPLE (ACER SACCHARUM MARSH.) AND RED MAPLE (ACER RUBRUM L.) TO INCREASING CONIFERS AND SOIL ACIDITY AS DEMONSTRATED BY FOLIAR NUTRIENT BALANCES

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## 3.1 Abstract

Sugar maple (*Acer saccharum* Marshall, SM) is believed to be more sensitive to acidic and nutrient-poor soils associated with conifer-dominated stands than red maple (*Acer rubrum* L., RM). Greater foliar nutrient use efficiency (FNUE) of RM is likely the cause for this difference. In the context of climate change, this greater FNUE could be key in favouring northward migration of RM over SM. We used the concept of foliar nutrient balances to study the nutrition of SM and RM seedlings along an increasing gradient in forest floor acidity conditioned by increasing proportions of conifers (pH values ranging from 4.39 under hardwoods, to 4.29 under mixed hardwood-conifer stands and 4.05 under conifer-dominated stands). Nutrients were subjected to isometric log-ratio (*ilr*) transformation, which views the leaf as one closed system and considers interactions between nutrients. The *ilr* method eliminates numerical biases and weak statistical inferences based on raw or "operationally'' log-transformed data. We analyzed foliar nutrients of SM and RM seedlings and found that the [Ca,Mg,K|P,N] and [Ca,Mg|K] balances of SM seedlings were significantly different among soil acidity levels, whereas they did not vary for RM seedlings. For SM seedlings, these differences among soil acidity levels were due to a significant decrease in foliar Ca and Mg concentrations with increasing forest floor acidity. Similar differences in foliar balances were also found between healthy and declining SM stands estimated from literature values. Conversely, foliar balances of RM seedlings did not differ among soil acidity levels, even though untransformed foliar nutrient concentrations were significantly different. This result highlights the importance of using *ilr* transformation, since it provides more sensitive results than standard testing of untransformed nutrient concentrations. The lower nutrient requirements of RM and its greater capacity to maintain nutrient equilibrium are factors that could explain its competitive success and recent northward expansion.

This study underscores the importance of using nutrient balances to study the redistribution of plant species in natural ecosystems under climate change.

**Key words**: seedlings, isometric log-ratio, conifers, soil acidity, ecological gradient, foliar nutrients.

## 3.2 Introduction

Climate, soil properties and biotic interactions are key factors controlling the geographical distribution of plant species (Whittaker, 1970). However, rapid ongoing climatic changes are creating new physiological constraints that force plant species to find new ecological optima by shifting their ranges to higher elevations and latitudes (Parmesan and Yohe, 2003; Rosenzweig et al., 2008; Chen et al., 2011). Scientists have paid greater attention to climate, as it is presumed to be the leading factor that results in changing plant distributions, but observed shifts of plant species have occurred at slower rates than that of climate change itself (Parmesan and Yohe, 2003; Loarie et al., 2009; Chen et al., 2011; Zhu et al., 2012). Recent evidence suggests that non-climatic factors such as soil properties and biotic interactions are slowing the migration of plant species (McMahon et al., 2011; Brown and Vellend, 2014; Graignic et al., 2014). Therefore, more research is needed regarding the role of non-climatic factors, such as soil properties, in affecting the northward migration of trees in the early stages of establishment (i.e., tree recruitment, including seed germination and seedling survival and growth) (Cleavitt et al., 2014).

Recruitment of sugar maple (*Acer saccharum* Marshall, SM) is of particular interest in eastern North America, given that this tree species is dominant over a large geographical area. Sugar maple is sensitive to acidic and nutrient-poor soils (St. Clair et al., 2008), and this sensitivity was proposed as an explanation for its limited

capacity in migrating northward into the boreal forest (Graignic et al., 2014). Acidic, Ca-poor soils that have thick litter layers, and which are characterized by low N-mineralization rates, generally support boreal forests (Binkley and Giardina, 1998). These soils may negatively affect the early stages of SM seedling establishment (Graignic et al., 2014), as has been demonstrated in various mature SM stands in eastern North America (Kobe et al., 2002; Juice et al., 2006; Long et al., 2009). The effects of soil acidity and soil base-cation depletion have resulted in foliar Ca and Mg deficiency, leading to tree decline.

Unlike SM, the range of red maple (*Acer rubrum* L., RM) has expanded more successfully over the last 100 years in North American forests that are supported by acidic and nutrient-poor soils (Abrams, 1998). Recently, Zhang et al. (2015) reported that RM establishment and growth were facilitated at its northern distributional limit in Quebec by increasing fire frequency. A survey of Allegheny National Forest (northwest Pennsylvania) revealed that decline symptoms and mortality rates in SM were three times greater than those of RM (McWilliams, 1996). These declines were linked to soil nutrient status (i.e., low Ca and Mg saturation) and severe insect defoliation events (Bailey et al., 2004). Variation in foliar nutrient use efficiency (FNUE) and tolerance to nutrient limitations were proposed as an explanation for the greater success of RM compared to SM on acidic and nutrient-poor soils (Abrams, 1998; St. Clair and Lynch, 2005c).

Relationships between soil nutrient availability, foliar nutrition and forest stand composition must be better understood to predict the recruitment and establishment of tree species that would need to migrate under climate change. Foliar nutrient status of forest tree species have been most often compared using mass nutrient content, nutrient percentages or dual ratios. However, foliar nutrients (as is the case of any other variables that are expressed in the same units, as proportions, percentages, ppm or ppb) belong to the class of compositional data, which are quantitative descriptions of the parts of a closed system, i.e., a composition or

simplex, within the leaf tissue (Aitchison, 1986). Such data consist of "closed" or bounded variables, since they sum to a constant value for a given sample. Thus, the manner in which foliar nutrients are reported has some consequences for their interpretation. First, the use of ratios can lead to spurious correlations caused by scaling as it was demonstrated that if the foliar nutrients *X*, *Y* and *Z* are uncorrelated, then *X*/*Z* and *Y*/*Z* will not be uncorrelated (Pearson, 1897; Chayes, 1960). Second, nutrients in the leaf are not only related physiologically through interactions (Marschner, 2011), but they are also numerically related given that all nutrients are constrained to sum to 100%; when one nutrient increases, then the others or some of the other nutrients must decrease concomitantly, and vice versa (Aitchison, 1986). Third, a *D*-part composition (*D* is the number of nutrients that have measured) has only *D*-1 degrees-of-freedom because one component can be calculated as the difference between the unit and the sum of the other components (Claringbold, 1955; Schrevens and Cornell, 1993;Aitchison and Greenacre, 2002). Using raw compositional data or dual ratios to conduct linear statistical analysis therefore leads to methodological biases and analytical incoherence caused by: (1) spurious correlations; (2) neglecting to account for nutrient interactions; and (3) redundancy of information that is carried by excess degrees-of-freedom (Wilkinson et al., 2000;Bacon-Shone, 2011). To avoid bias, the isometric log-ratio (*ilr*) transformation technique that was developed by Egozcue (2003) allows $D - 1$ orthogonal contrasts to be produced, which are interpreted as balances between two groups of nutrients in an Euclidean space. The *ilr* transformation also illustrates nutrient relationships according to partitions that decompose the composition into hierarchically arranged or nested groups of nutrients, i.e., subcompositions (Parent et al., 2012b). Further, *ilr* is the most appropriate transformation and easily interpreted for plant nutrient diagnosis (Parent, 2011; Parent et al., 2012a; Parent et al., 2013), compared to additive log-ratios or centred log-ratios. Our objective was to use *ilr*-transformed foliar nutrients to study the nutrition of SM and RM seedlings along a gradient of soil

acidity conditioned by increasing proportions of conifers. We hypothesized that while nutrient imbalances in SM foliage are exacerbated due to increasing soil acidity, nutrients in RM foliage are more balanced because this species can better adapt to environments with greater nutrient limitations.

## 3.3 Materials and Methods

### 3.3.1 Study site

The study site is located at the *Station de Biologie des Laurentides* (SBL) of the *University de Montréal* in St. Hippolyte, Quebec (45°59'N; 74°00'O). The SBL lies within the SM-yellow birch (*Betula alleghaniensis* Britton) domain of the lower Laurentians, near its northern limit and at the transition with the boreal forest (Saucier et al., 2009). Sugar maple is found concurrently with RM, yellow birch, poplars (*Populus* spp.), balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* [Moench] Voss) and eastern white cedar (*Thuja occidentalis* L.). Due to the mosaic of tree species that formed the site, it was possible to find SM and RM seedlings growing concomitantly along an increasing gradient of soil acidity conditioned by increasing proportions of coniferous tree species.

### 3.3.2 Experimental design and sampling

Plots that were used for this experiment are the same as those previously studied in Chapter I (see Appendix A). Four plots (50 × 50 m) were delineated under each of the following forest canopies: (1) hardwood stands of SM and birch species; (2) mixed hardwood-conifer stands with SM, *Betula* spp. and conifers; and (3) conifer-dominated stands with SM seedlings and saplings (3 sites × 3 species composition × 4 repetitions = 36 plots). In each of these plots, SM and RM seedlings were present. Foliage from five SM and RM seedlings (between 20 and 30 cm in

height) were collected within each plot for subsequent chemical analysis. Total height and diameter at the ground level were measured on all SM and RM seedlings that were sampled. We did not measure the age of SM and RM seedlings, but we assume that SM seedlings were a little bit older than RM seedlings, on average, due to their greater shade-tolerance and slower growth rate. However, nutrient concentrations in plant parts are mostly affected by their physiological age (Marschner, 2011). Therefore, comparisons of nutrient concentrations and ratios should ideally be done between plants of similar growth stages and not necessarily of similar ages. In this respect, the bias that was incurred by comparing SM and RM of similar heights and growth stages, despite possible differences in ages, is likely small.

The sandy loam soils at St. Hippolyte are Orthic Humo-Ferric Podzols (Soil Classification Working Group, 1998) developed from well-drained rocky glacial tills composed of a mixture of rocks from the small underlying anorthosite pluton (deep-seated intrusive igneous rock) of the Morin Complex (Doig, 1991) and of more felsic rocks (e.g. mangerite, syenite, charnockite) in the surroundings of the anorthosite pluton (Bélanger et al. 2012). The forest floor is a moder humus form with a thickness of 5 to 10 cm. Details on soil sampling, analysis and chemical properties are provided in Collin et al. (submitted). We simply confirm here that conifer-dominated stands have a significantly lower forest floor (i.e. FH horizons) pH (4.05 ±0.07) compared to forest floors supporting mixed hardwood-conifer stands (4.29 ±0.11) and hardwoods (4.39 ±0.09). On the whole, nothing indicates that variations in forest floor pH are due to intrinsic site factors (e.g., parent material and topographic position, slope or aspect) other than forest type. For example, mineral soil texture is similar under each of the forest canopies and composed of about 2-3% of clay, 38-42% of silt and 55-60% of sand.

### 3.3.3 Foliar nutrients

Leaf samples were oven-dried for 72 h at 65 °C upon arrival in the laboratory. They were then pulverized using a ball mill prior to total C and N determination by high-temperature combustion and infrared detection (EA 1108 CHNS-O Analyzer, Thermo Fisons, Waltham, MA, USA). A 0.2 g subsample was also digested in 2 ml of 15 N $HNO_3$ for 4 h at 100 °C in glass test tubes. Base cation concentrations (Ca, Mg and K) of the digests were determined using atomic adsorption/emission (Model AA-1475, Varian, Palo Alta, CA, USA), whereas P concentrations were determined colorimetrically using the molybdenum blue method (Technicon Autoanalyzer, Technicon Instruments Corporation, Tarrytown, NY, USA).

### 3.3.4 Computation of foliar nutrient *ilr* balances

Computing *ilr* implies that the compositional data are numerically constrained to a compositional data space. Given that not all elements of the leaf are typically measured, it is therefore a necessity to first compute a filling value (*Fv*), which replaces the elements that were not measured. This *Fv* was calculated as the difference between the unit of measurement (i.e., 100%) and the sum of all nutrients that had been measured. The compositional data matrix was then constrained as described by Aitchison (1986), i.e., the closure operation computes the constant sum of components and closes it to some whole such as 100%. Once the composition data space was closed, the *ilr*-transformation was applied (Egozcue et al., 2003). This *ilr* system of balances is first defined by a nested, binary contrasts that are implemented during the sequential binary partition (SBP) steps, in which components are hierarchically arranged into functional sub-compositions (Parent et al., 2012b). This hierarchical arrangement of balances needs to be constructed based on prior knowledge or hypotheses as a means to produce interpretable results (Parent et al., 2012b). In this study, the SBP (Table 3.1) was designed based on prior knowledge of

nutrient interactions in higher plants (Marschner, 2011). We first contrasted all measured nutrients (i.e., N, P, K, Ca and Mg) with *Fv*, i.e. [Fv | Elements]. We then partitioned measured nutrients to reflect the charge balance in plant cells (Marschner, 2011). Thus, N and P were contrasted with K, Ca and Mg, i.e., the two-part amalgamated ratio [Mg,Ca,K | P,N]. Sub-compositions were further divided into an anionic Redfield [P | N] balance (Loladze and Elser, 2011) and cationic [Mg,Ca | K] and [Mg | Ca] balances (Marschner, 2011).

**Table 3.1** Sequential binary partition (SBP) of foliar nutrients of sugar and red maple seedlings based on prior knowledge of nutrient interactions in higher plants (Marschner 2011).

| Balance [-1 subset \| +1 subset] | N | P | K | Ca | Mg | Fv | $n^+$ | $n^-$ |
|---|---|---|---|---|---|---|---|---|
| [Fv \| N, P, K, Ca, Mg] | 1 | 1 | 1 | 1 | 1 | -1 | 5 | 1 |
| [K, Ca, Mg \| N, P] | 1 | 1 | -1 | -1 | -1 | 0 | 2 | 3 |
| [P \| N] | 1 | -1 | 0 | 0 | 0 | 0 | 1 | 1 |
| [Ca, Mg \| K] | 0 | 0 | 1 | -1 | -1 | 0 | 1 | 2 |
| [Mg \| Ca] | 0 | 0 | 0 | 1 | -1 | 0 | 1 | 1 |

The composition is partitioned sequentially and hierarchically into subcompositions where parts labelled "1" at numerator are contrasted with parts labelled "-1" at denominator in each row. Parts labelled "0" are excluded from the contrast. Balances are noted with denominator placed on the left because log ratios become more negative as values at denominator increase, hence leaning to the left as in algebra.

The *ilr* balances defined during the SBP steps (Table 3.1) were then computed according to the equation by Egozcue and Pawlowsky-Glahn (2005):

$$ilr_j = \sqrt{\frac{n_j^+ n_j^-}{n_j^+ + n_j^-}} ln \frac{g(c_j^+)}{g(c_j^-)}$$

where, in the $j^{th}$ row of the SBP, $n_j^+$ and $n_j^-$ are the numbers of components in the plus (+) and minus (–) groups, and $g(c_j^+)$ and $g(c_j^-)$ are the geometric means of components in the "+" and "–" group, respectively. Balances are generally noted [-1 group | +1 group], with denominator on the left because log ratios become more negative as values at denominator increase, hence leaning to the left as in algebra. For example, the *ilr* equation of the [Mg|Ca] partition is $\sqrt{\frac{1}{2}} ln \frac{Ca}{Mg}$. If Ca concentration increases, then the *ilr* coordinate will also increase in value. In addition, an increase in Ca concentration will change the [Mg|Ca] and [Mg,Ca|K] balances, without affecting the [P|N] balance. This technique produces *D*-1 balances in a *D*-part composition, avoiding matrix singularity and redundancy. The transformation also assures that *ilr* are orthogonal to each other, thus linearly independent, making this technique totally appropriate for conducting multivariate and multiple regression analyses.

### 3.3.5 Computation of foliar nutrient ranges of SM and RM

Because growth rates of maple seedlings were not measured in this study, we could not directly assess their health and vigour in relation to foliar nutrients. Therefore, we compared foliar data obtained from the literature to foliar data from SM seedlings at St. Hippolyte to assess their nutritional status. First, foliar nutrient concentrations that were measured in this study were compared to foliar nutrient concentrations from a small set of recent literature reports that included data on SM and RM seedlings that were growing on similar acidic soils (forest floor pH ranging

from 3.4 to 5.5). The data were used to construct ranges of foliar N, P, K, Ca and Mg concentrations. Second, we attempted to develop specific ranges for foliar *ilr* balances in healthy and declining maple seedlings from the literature. However, data on foliar nutrients for SM and RM seedlings are sparse. Many studies do not report all foliar nutrients that are required to compute *ilr* balances, nor do they relate foliar nutrients to seedling performance. Foliar nutrient concentrations of SM trees are more widely documented and relationships to tree fitness are often provided. A substantial SM database comprised of trees growing on soils (forest floors) with pH values ranging from 3.14 to 7.04 was assembled, which allowed us to construct ranges in foliar *ilr* balances for healthy and declining SM stands. This data set was later used as a proxy for the nutritional status of SM seedlings that were growing under three different forest types (hardwood, mixed hardwood-conifer and conifer-dominated forests) at St. Hippolyte. Conversely, foliar nutrient data for RM are sparse for both trees and seedlings and, in turn, it was not possible to compute foliar *ilr* balances for RM.

### 3.3.6 Statistical analyses

Data were analyzed using R software (version 3.0.0, R Core Development Team, 2015). The *ilr*-transformations were performed with the functions *acomp* and *ilr* of the *compositions* package (van den Boogaart et al., 2013). The function *acomp* is used for the closure operation, and the function *ilr* is used on this closed data space to perform the *ilr* transformation equation described above. To assess whether forest types have specific foliar nutrition signatures, linear discriminant analysis combined with a posteriori classification was performed with the function *lda* available in the *MASS* package (Venables and Ripley, 2002). Foliar *ilr* balances were employed as the response variables, and the multivariate homogeneity of variance-covariance matrices (permutation-based, multivariate extension of Levene's test) between species was

tested using the *betadisper* function in the *vegan* package (Oksanen et al., 2013). Multivariate regressions between foliar signatures as the response variables (i.e., all balances considered) and forest floor pH as the explanatory variable were computed using data from all forest types to determine if foliar balances of SM or RM seedlings are controlled by forest species composition. Simple linear regressions between each foliar *ilr* balance and forest floor pH were then performed to quantify the relative contributions of each balance to the main multivariable SM and RM regressions if the latter were found significant. One-way analysis of variance and Tukey's HSD (honest significant difference) post-hoc tests were also used to separate means of forest types or species based on their respective mean foliar nutrient concentrations and balances. Testing nutrient concentrations aided our interpretation of nutrient balance results. Foliar nutrient concentrations that were used in the analysis were occasionally log-transformed to meet the assumptions of normality and homoscedasticity of the residuals.

## 3.4 Results

### 3.4.1 Foliar nutrient concentrations

Concentrations of foliar N, P, K, Ca and Mg of SM and RM seedlings among the three forest types at St. Hippolyte are presented in Table 3.2. Sugar maple seedlings that were sampled in hardwood stands have significantly higher foliar Ca and Mg concentrations than seedlings in conifer-dominated stands. Foliar K concentrations of RM seedlings in hardwood stands are significantly higher than seedlings in conifer-dominated stands. Also, RM seedlings in mixed hardwood-conifer stands have significantly higher foliar N concentrations than seedlings in conifer-dominated stands. Finally, RM seedlings have significantly lower foliar N and higher foliar Mg concentrations than SM seedlings (Table 3.2).

Foliar nutrient concentrations in SM and RM seedlings that were measured in St. Hippolyte are generally within the range of concentrations that have been reported in the recent literature (Figure 3.1). Only foliar P concentrations of both SM and RM seedlings are at the lower limit of literature ranges.

**Table 3.2** Mean foliar nutrient concentrations (%) of sugar maple and red maple seedlings between forest types. Standard errors are presented in parentheses.

| | N | P | K | Ca | Mg |
|---|---|---|---|---|---|
| Sugar maple | | | | | |
| Hardwood | 1.88 (± 0.10) | 0.11 (± 0.01) | 0.63 (± 0.07) | 0.91 (± 0.06) **a** | 0.21 (± 0.03) **a** |
| Mixed hardwood-conifer | 1.71 (± 0.10) | 0.11 (± 0.005) | 0.60 (± 0.08) | 0.84 (± 0.06) **ab** | 0.19 (± 0.02) **ab** |
| Conifer-dominated | 1.86 (± 0.14) | 0.11 (± 0.01) | 0.65 (± 0.06) | 0.74 (± 0.06) **b** | 0.16 (± 0.02) **b** |
| Red maple | | | | | |
| Hardwoods | 1.64 (± 0.07) **ab** | 0.11 (± 0.01) | 0.78 (± 0.13) **a** | 0.86 (± 0.11) | 0.34 (± 0.03) |
| Mixed hardwood-conifer | 1.74 (± 0.13) **a** | 0.11 (± 0.004) | 0.70 (± 0.07) **ab** | 0.75 (± 0.05) | 0.31 (± 0.03) |
| Conifer-dominated | 1.52 (± 0.08) **b** | 0.11 (± 0.01) | 0.59 (± 0.06) **b** | 0.78 (± 0.08) | 0.30 (± 0.02) |
| Species comparison | | | | | |
| *P*-value | < 0.001 | 0.977 | 0.116 | 0.328 | < 0.001 |

Note: Means within a column for a given species that are followed by the same letter do not differ at $P < 0.05$ (Tukey tests). Species comparisons consider forest type as a random factor.

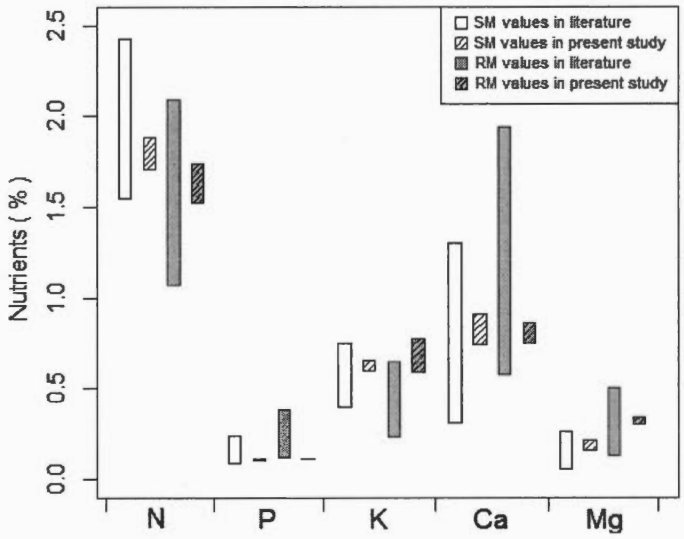


**Figure 3.1** Ranges of foliar N, P, K, Ca and Mg concentrations in sugar maple (SM) and red maple (RM) seedlings that were measured in this study and were taken from the literature, i.e., based on St. Clair and Lynch (2005a), St. Clair and Lynch (2005c), Park and Yanai (2009), Fahey and Blum (2011), Momen et al. (2015).

**Table 3.3** Mean foliar *ilr* balances of sugar maple and red maple seedlings among forest types. Standard errors are presented in parentheses.

| | Ilr Balances | | | | |
|---|---|---|---|---|---|
| | [Fv\|Elements] | [Mg,Ca,K\|P,N] | [P\|N] | [Mg,Ca\|K] | [Mg\|Ca] |
| Sugar maple | | | | | |
| Hardwood | -4.86 (± 0.05) | -0.06 (± 0.08) | 1.99 (± 0.05) | 0.28 (± 0.10) | 1.05 (± 0.08) |
| Mixed hardwood-conifer | -4.93 (± 0.05) | -0.06 (± 0.06) | 1.96 (± 0.03) | 0.31 (± 0.14) | 1.06 (± 0.07) |
| Conifer-dominated | -4.95 (± 0.05) | 0.11 (± 0.05) | 1.98 (± 0.06) | 0.54 (± 0.12) | 1.13 (± 0.12) |
| Red maple | | | | | |
| Hardwoods | -4.83 (± 0.16) | -0.33 (± 0.15) | 1.96 (± 0.16) | 0.25 (± 0.11) | 0.65 (± 0.08) |
| Mixed hardwood-conifer | -4.82 (± 0.04) | -0.23 (± 0.08) | 1.95 (± 0.06) | 0.30 (± 0.08) | 0.64 (± 0.07) |
| Conifer-dominated | -4.88 (± 0.03) | -0.23 (± 0.06) | 1.85 (± 0.06) | 0.15 (± 0.11) | 0.66 (± 0.09) |

### 3.4.2 Foliar *ilr* balances

Foliar *ilr* balances of SM and RM seedlings at St. Hippolyte were computed for each forest type (Table 3.3). Considering the influence of forest type on soil chemical properties (notably forest floor pH, see Chapter I), it was necessary to analyze the data using a mixed-effects model to separate the plot and forest type effects on the foliar balances of SM and RM. Analysis revealed that SM seedlings have significantly higher foliar [Mg,Ca,K|P,N], [Mg,Ca|K] and [Mg|Ca] balances, and a significantly lower foliar [Fv|Elements] balance compared to RM (Figure 3.2). It is important to note that these balances do not behave in the same manner as traditional ratios. A decreasing foliar *ilr* balance means that either the left part of the balance (the numerator of the ratio) is increasing or that the right part (the denominator of the ratio) is decreasing. Linear discriminant analysis suggests that the foliar [Mg|Ca] balance, followed by the [Mg,Ca,K|P,N] balance, can discriminate most RM seedlings from SM seedlings (Figure 3.3). The resulting classification matrix indicated 91.6 % and 85 % correct classifications of SM and RM seedlings, respectively, using foliar balances. This indicates that foliage of SM and RM seedlings possess distinct nutritional signatures.

Foliar [Mg,Ca,K|P,N] and [Mg,Ca|K] balances of SM seedlings rise with increasing proportions of conifers (and thus, increasing forest floor acidity) (Figure 3.4). These balances are significantly higher for seedlings in conifer-dominated stands than for seedlings in hardwood stands. Conversely, the foliar [Fv|Elements] balance of seedlings in conifer-dominated stands is significantly lower than that for seedlings in hardwood stands. No difference was found among forest types in the foliar balances that were computed for RM. A high degree of variability was found for the balances of RM seedlings in hardwood stands (Table 3.3, Figure 3.4).

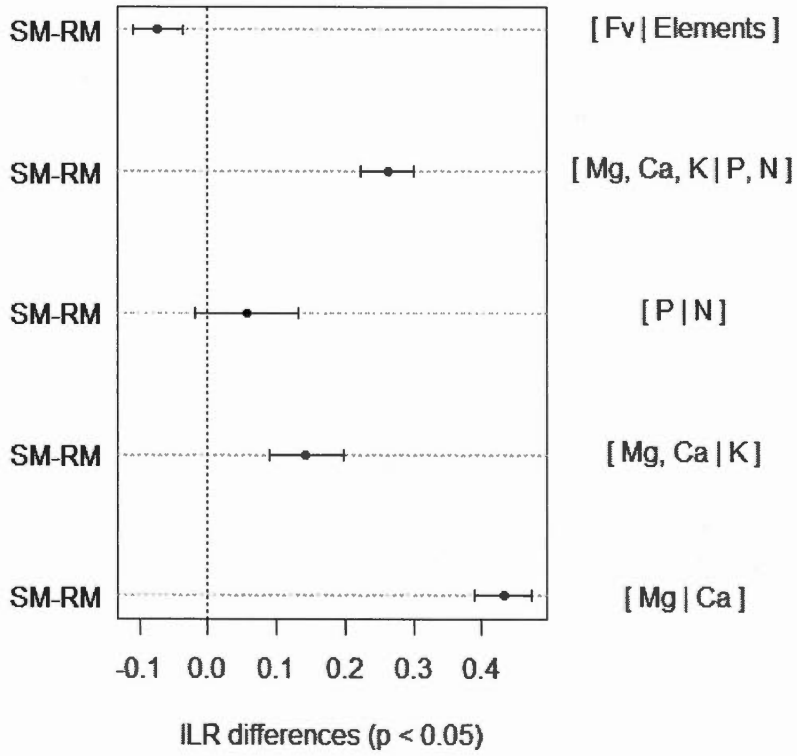


**Figure 3.2** Tukey tests determined differences in foliar *ilr* balances between sugar maple (SM) and red maple (RM) seedlings, as analyzed using a mixed model with plot and forest type as random factors. Differences are significant ($P < 0.05$) when they do not include zero. Differences on the left side of the origin indicate that concentrations of nutrients in the left part of the balance are higher (or concentrations in right part lower) in SM than RM seedlings, and vice-versa.

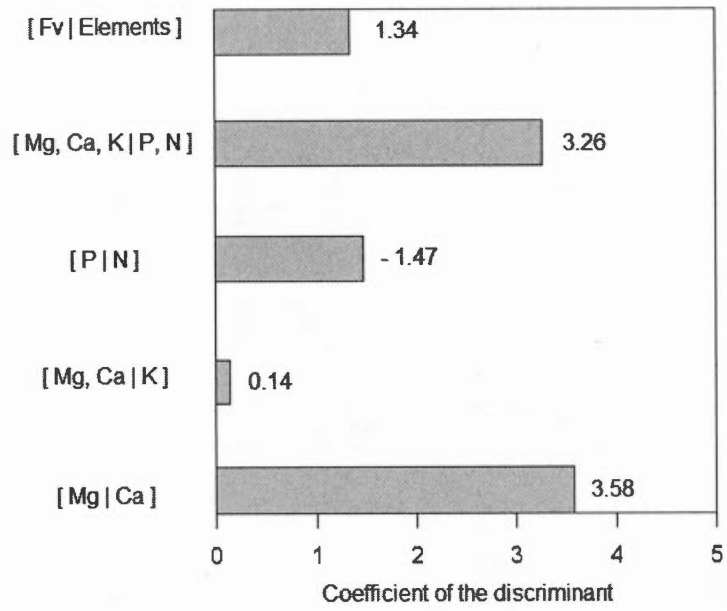


**Figure 3.3** Results of linear discriminant function analysis (DFA) between foliar balances of sugar maple (SM) and red maple (RM) seedlings. The 1st axis explains all of the variation. Subsequent classification analysis reports that 91.6 and 85 % of responses were correctly classified for SM and RM seedlings, respectively. The higher the absolute value of the coefficient, the higher its ability to discriminate between groups.

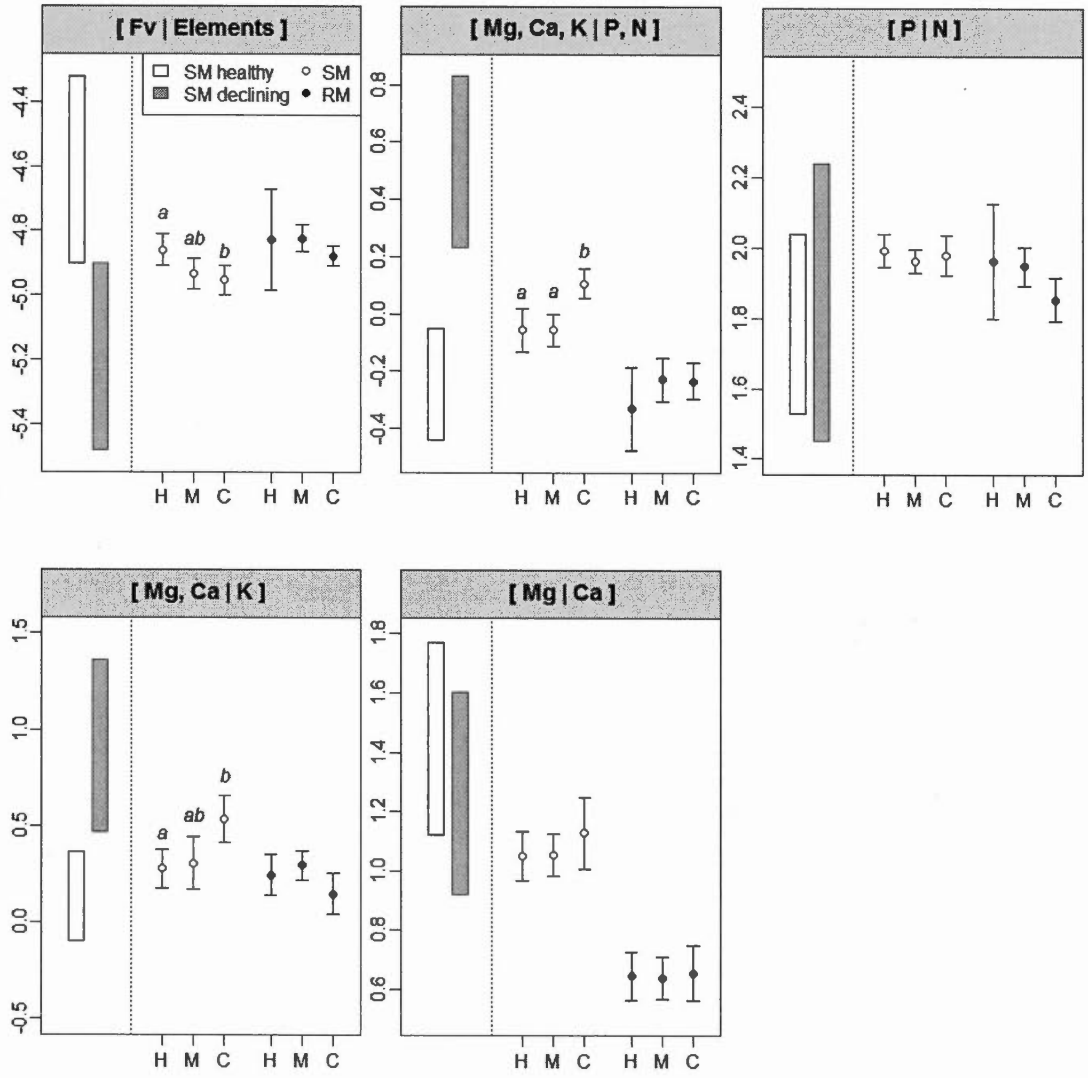


**Figure 3.4** Comparison of foliar *ilr* balances of sugar maple (SM) and red maple (RM) seedlings among forest types (H: hardwood stands, M: mixed hardwood-conifer stands, C: conifer-dominated stands). Rectangles on the left of each panel are foliar *ilr* balances based on literature data for healthy and declining SM stands (see Table 5 for details of references and values). Significant differences ($P < 0.05$) in foliar balances between forest types (not between maple species) are indicated with different letters. A significantly lower balance indicates that concentrations of nutrients in the left part of the balance are significantly higher (or concentrations in right part lower), and vice-versa.

A significant linear relationship was found between foliar signatures (i.e., all balances considered) of SM seedlings and forest floor pH which varied with forest types (adjusted $R^2$ = 0.262, $P$ < 0.01, Table 3.4). However, this relationship is only due to variations in foliar [Mg,Ca|K] balances (adjusted $R^2$ = 0.494, $P$ < 0.01). There is no relationship between foliar signatures of RM seedlings and forest floor pH (adjusted $R^2$ = -0.056, $P$ = 0.83, Table 3.4). This is in agreement with the observation that foliar balances of RM seedlings do not vary significantly among forest types.

**Table 3.4** Linear model comparisons between foliar *ilr* balances (response variables) of sugar and red maple seedlings and forest floor pH. Significant model fits are indicated by *P*-values in bold type.

| | $R^2$ | adjusted $R^2$ | Var | $F$-value | $P$-value |
|---|---|---|---|---|---|
| Sugar maple | | | | | |
| *all ilr* | 0.33 | 0.26 | 0.025 | 4.91 | **0.005** |
| *(1) [Fv\|Elements]* | 0.06 | -0.04 | 0.0003 | 0.59 | 0.45 |
| *(2) [Mg,Ca,K\|P,N]* | 0.22 | 0.14 | 0.003 | 2.81 | 0.13 |
| *(3) [P\|N]* | 0.01 | -0.10 | 0.00003 | 0.04 | 0.84 |
| *(4) [Mg,Ca\|K]* | 0.54 | 0.49 | 0.022 | 11.7 | **0.006** |
| *(5) [Mg\|Ca]* | 0.03 | -0.06 | 0.0003 | 0.35 | 0.59 |
| *(1+2+4)* | 0.43 | 0.37 | 0.025 | 7.41 | **0.01** |
| *(2+4)* | 0.47 | 0.41 | 0.024 | 8.79 | **0.005** |
| Red maple | | | | | |
| *all ilr* | 0.04 | -0.06 | 0.0052 | 0.42 | 0.83 |

### 3.4.3 Comparison of foliar *ilr* balances of SM seedlings within healthy and declining stands

Foliar *ilr* balances for healthy and declining SM stands that were computed from literature foliar nutrient data are presented in Table 3.5. The ranges of those foliar balances are represented in Figure 3.4, together with foliar *ilr* balances of SM seedlings at St. Hippolyte. Comparisons between datasets can be used to partially assess SM seedling fitness. On the one hand, foliar [Mg,Ca,K|P,N] and [Mg,Ca|K] balances of declining SM stands are higher than foliar balances of healthy stands. On the other hand, foliar [Fv|Elements] balances are lower for declining SM stands than healthy stands. Among these three balances diverging between healthy and declining stands, foliar [Fv|Elements] of SM seedlings in mixed hardwood-conifer and conifer-dominated stands at St. Hippolyte fall within the upper limit of declining stands, whereas foliar [Fv|Elements] of SM seedlings in hardwood stands fall within the range of healthy stands. Foliar [Mg,Ca|K] and [Mg,Ca,K|P,N] balances of SM seedlings in hardwood and mixed hardwood-conifer stands fall within the upper limit of the ranges of healthy stands, whereas the balances of seedlings in conifer-dominated stands fall within or lean towards the lower limit of declining stands for [Mg,Ca|K] and [Mg,Ca,K|P,N], respectively.

**Table 3.5** Foliar *ilr* balances that were computed based on nutrient concentrations found in the literature for healthy and declining sugar maple trees.

| Source | Isometric Log Ratios balances | | | | |
|---|---|---|---|---|---|
| | [Fv\|Mg,Ca,K,P,N] | [Mg,Ca,K\|P,N] | [P\|N] | [Mg,Ca\|K] | [Mg\|Ca] |
| | **Healthy stands** | | | | |
| Lozano & Huynh (1989) | -4.56 | -0.25 | 1.53 | -0.10 | 1.77 |
| Kolb & McCormick (1993) | -4.32 | -0.44 | 1.81 | 0.09 | 1.20 |
| Côté & Camiré (1995) | -4.59 | -0.15 | 1.90 | 0.08 | 1.38 |
| Ouimet & Camiré (1995) | -4.80 | -0.06 | 1.93 | 0.21 | 1.30 |
| Liu, Ellsworth & Tyree (1997) | -4.90 | -0.11 | 2.04 | 0.11 | 1.28 |
| Moore, Duchesne & Ouimet (2008) | -4.70 | -0.05 | 1.80 | 0.04 | 1.12 |
| Long et al. (2009) | -4.35 | -0.16 | 1.59 | 0.33 | 1.66 |
| | -4.39 | -0.17 | 1.58 | 0.37 | 1.32 |
| **Mean - Healthy Stands** | -4.58 | -0.17 | 1.77 | 0.14 | 1.38 |
| | **Declining Stands** | | | | |
| Lozano & Huynh (1989) | -5.24 | 0.57 | 1.92 | 1.08 | 1.20 |
| | -5.04 | 0.83 | 1.45 | 1.06 | 1.60 |
| Kolb & McCormick (1993) | -4.95 | 0.48 | 1.95 | 0.75 | 1.52 |
| | -5.26 | 0.68 | 2.10 | 1.36 | 1.42 |
| Côté & Camiré (1995) | -5.05 | 0.44 | 2.24 | 0.77 | 1.54 |
| | -5.01 | 0.28 | 2.03 | 0.75 | 1.38 |
| Ouimet & Camiré (1995) | -4.90 | 0.35 | 1.87 | 0.47 | 0.92 |
| Liu, Ellsworth & Tyree (1997) | -4.97 | 0.23 | 1.73 | 0.69 | 1.38 |
| Moore & Ouimet (2006) | -5.02 | 0.58 | 1.85 | 0.89 | 1.03 |
| Moore, Duchesne & Ouimet (2008) | -5.07 | 0.51 | 1.74 | 0.96 | 1.08 |
| Long et al. (2009) | -5.48 | 0.57 | 1.80 | 1.19 | 1.37 |
| | -5.41 | 0.68 | 1.96 | 1.20 | 1.29 |
| **Mean - Declining Stands** | -4.90 | 0.83 | 2.24 | 1.36 | 1.60 |

## 3.5 Discussion

We tested the hypothesis that while nutrient imbalances in SM seedling foliage increase with increasing soil acidity, nutrients in RM seedling foliage are more balanced because this species can better adapt to environments with greater nutrient limitations. Thus, *ilr* balances were computed from foliar nutrient concentrations of SM and RM seedlings that were growing naturally on forest floors with increasing acidity as conditioned by varying proportions of conifers. Our results support both parts of the hypothesis.

### 3.5.1 Foliar *ilr* balances

Differences in foliar [Mg|Ca] and [Mg,Ca,K|P,N] balances between SM and RM seedlings directly reflect foliar concentrations of N and Mg in RM seedlings, which are respectively lower and higher than those of SM seedlings (Table 3.2). Higher foliar Mg concentrations tend to lower the [Mg|Ca] balance, whereas lower N concentrations tend to lower the [Mg,Ca,K|P,N] balance. Concentrations of foliar nutrients in RM seedlings were previously reported as being lower than those of SM seedlings in ecosystems that are characterized by acidic soils, according to St. Clair and Lynch (2005c). These authors explained that lower nutrients in RM foliage could be due, in part, to lower nutrient requirements of RM. However, at St. Hippolyte, foliar nutrients of RM seedlings were not necessarily lower than those of SM seedlings. Moreover, foliar nutrients of SM and RM seedlings at our study site were generally in the same range as values that have been reported in other recent studies for SM and RM seedlings (Figure 3.1), reinforcing the idea that seedlings of various ages can be compared relatively well as long as they have similar physiological ages (Marschner, 2011).

Back-transformations of foliar [P|N] balances to N:P ratios at St. Hippolyte yielded values averaging 16.6 (± 0.6) for SM seedlings and 17.5 (± 4.5) for RM

seedlings (data not shown). A meta-analysis of Redfield ratios of terrestrial plant species in natural field sites revealed an average value of 12-13 (Güsewell, 2004). N:P ratios vary widely among and within species, with intraspecific variation being greater than interspecific variation. Ratios <10 and >20 generally correspond respectively to N- and P-limited biomass production (Güsewell, 2004). The higher average N:P ratio in St. Hippolyte compared to the mean ratio that was reported by Güsewell (2004) is most likely the consequence of the low foliar P concentrations at our study site. Foliar P concentrations of both SM and RM seedlings at St. Hippolyte are at the lower limit of values that are reported in the literature (Figure 1). This could be due to the fact that both species are at the northern limits of their distributions. Lower soil temperatures that are found at the northern limit tend to decrease nutrient turnover and availability (Zak et al., 1999), and ion uptake by plant roots (Dong et al., 2001; Pregitzer and King, 2005). However, we believe that low foliar P concentrations at St. Hippolyte are more likely related to its very specific bedrock and parent material geochemistry (see Materials and Methods section for details), which in turn affect soil P availability and plant uptake. As a whole, the podzolic B horizons have very low Mehlich III extractable P concentrations (average of 0.92 mg P $kg^{-1}$, Collin et al. submitted) and total $P_2O_5$ contents (~0.02%) (Bélanger et al. 2012).

### 3.5.2 Influence of forest type

Increasing proportions of conifers and soil acidity resulted in modifications of foliar *ilr* balances only for SM seedlings (Figure 3.4). A significant decline in the foliar [Fv|Elements] balance with an increasing proportion of conifers indicates a general decrease in nutrients or an increase in *Fv*. The *Fv* is composed of elements that are not often measured, particularly in forest studies, viz., C, H, O, other macronutrients (e.g., S) and micronutrients (e.g., Cu, Zn, B). An increase in foliar Al and Mn concentrations in SM seedlings under an increasing proportion of conifers

may be one factor explaining *Fv* variation. Increases in foliar Al and Mn have been recorded in SM due to decreasing soil pH (Hallett et al., 2006; Kogelmann and Sharpe, 2006; Schaberg et al., 2006; Long et al., 2009; Park and Yanai, 2009; Beauregard et al., 2010). High ionic activity of Al and Mn in acidic soil solution is common and this tends to increase their uptake by tree roots at the expense of Ca and Mg, including SM (Cronan and Grigal, 1995; Likens et al., 1998). A significant increase in the foliar [Mg,Ca,K|P,N] balance can be due to a decrease in Mg, Ca or K concentrations, or an increase in P and N concentrations. However, our data suggest that the latter explanation is compromised, as foliar N and P concentrations of SM seedlings did not vary between forest types (Table 3.2). Thus, the significantly higher foliar [Mg,Ca|K] balance of SM seedlings in conifer-dominated stands compared to SM seedlings in hardwood stands, together with stability of the foliar [Mg|Ca] balance between forest types, could mean that Ca and Mg are deficient in conifer-dominated stands compared to hardwood stands. The foliar [Mg,Ca|K] balance was also the main factor explaining foliar *ilr* balance discrimination among forest types (Table 3.4). Differences in foliar balances, therefore, are clearly related to decreasing soil pH and most probably increased Al and Mn mobility/availability. The latter are both conditioned by increasing proportions of conifers. In turn, there is an antagonistic effect on Ca and Mg uptake by SM seedlings that subsequently translates into foliar imbalances. These results support the first part of our hypothesis that nutrient imbalances in SM foliage increase due to increasing soil acidity as conditioned by increasing proportions of conifers.

It is well known that SM trees are particularly sensitive to low Ca and Mg availability compared to other tree species that are growing on acidic soils (Kobe et al., 2002; Duchesne and Ouimet, 2009; Long et al., 2009). Most declining SM stands in southern Quebec were attributed to low soil Ca and Mg availability, in part, due to imbalances in Al and Mn that were induced by atmospheric acid deposition. Imbalances could also be attributed to exports of Ca and Mg in harvested biomass in

excess of natural inputs, resulting in low foliar Ca and Mg (Duchesne et al., 2002; Ouimet et al., 2006; Duchesne and Ouimet, 2009). The health and vigour of SM trees is constrained by the low Ca and Mg availability of acidic soils, and accompanied by foliar Ca and Mg concentrations below deficiency thresholds (Drohan et al., 2002; Bailey et al., 2004; Houle et al., 2007; St. Clair et al., 2008; Long et al., 2009). Foliar Mg concentrations in declining SM stands are often very low and correlated with a decline in canopy health (Horsley et al., 2000). The benefits of liming declining stands of SM on rates of photosynthesis or growth were demonstrated through field studies (Liu et al., 1997; Duchesne et al., 2003; Moore and Ouimet, 2006; Schaberg et al., 2006; Moore et al., 2014). Calcium and Mg deficiencies of SM seedlings in conifer-dominated stands compared to hardwood stands at St. Hippolyte suggests that conifer-dominated boreal forests could limit the ability of SM to migrate northward to find a more adequate climate in a rapidly warming world. Our results only reflect the best-case scenario as the SM seedlings that were measured were those capable of naturally growing even under more stressful conditions that were found in conifer-dominated stands. Many conifer-dominated stands, for example, were not selected for the study because SM seedlings were not present. Similarly, the only foliar balances of SM seedlings that were significantly different among forest types at St. Hippolyte, i.e., [Fv|Elements], [Mg,Ca,K|P,N], [Mg,Ca|K] (Table 3.3, Figure 3.2), were also those differing between healthy and declining SM stands found in the literature (Table 3.4, Figure 3.4). Because the data linking yield, fitness and foliar nutrition is unfortunately limited to SM trees, not to SM seedlings, it is likely more appropriate to refer to samples in conifer-dominated stands as poorly acclimating seedlings rather than declining seedlings.

Foliar balances of RM seedlings at St. Hippolyte do not show any significant difference among forest types (Figure 3.4), nor are foliar balances related to forest floor pH (Table 3.5). These results indicate a greater capacity of RM seedlings to

maintain their foliar balances within a certain range of soil acidity (i.e., forest floor pH on the study site ranges from 3.73 to 4.94) than SM seedlings. Greater variation in foliar balances of RM seedlings in the hardwood stands may be the reason that we failed to detect significant differences among forest types. However, the large variation may also reflect higher nutritional plasticity in RM to contrasting environmental conditions. In the past few decades, RM populations in eastern North America have been expanding more rapidly than those of other tree species (Alderman et al., 2005; Fei and Steiner, 2007). Expansion of RM was related to factors as diverse as fire regime, climate, biotic interactions and physiological characteristics. For example, high recruitment capacity that is associated with high seed banking (and, therefore, fast colonization capacity) was proposed as an explanation for its current expansion (Warren et al., 2004; Lambers and Clark, 2005). Lower energy and resource requirements for biomass production and maintenance were also suggested to explain its competitive success (Nagel et al., 2002). As a whole, RM is characterized as a competitive generalist possessing functional traits belonging to both early and late-successional tree species (Abrams, 1998). It is able to thrive on sites with greatly contrasting soil conditions due to its lower water and nutrient requirements for growth and survival compared to many other hardwood species in North America. Our results support the second part of our hypothesis that suggests the lower nutrient requirements of RM seedlings allow the species to adapt nutritionally to a wide range of acid soils compared to SM seedlings. This lower nutrient requirement is another possible factor explaining the recent expansion of RM relative to SM on acidic and nutrient-poor soils.

## 3.6 Conclusion

First, our study indicates that forest floor acidity under conifer-dominated forests negatively affects foliar nutrition of SM seedlings through reduced foliar Ca and Mg concentrations. This leads to alteration of the equilibrium of foliar nutrient balances. In this case, analysis of foliar nutrient concentrations and balances led to similar conclusions. Second, results support our hypothesis that RM seedlings can better adapt its foliar nutrient balances than can SM seedlings through greater tolerance of more acidic soil environments with lower nutrient availability. Interestingly, while RM balances were not significantly different between forest types, foliar nutrient concentrations showed statistically significant decreases with traditional mean comparison (i.e. N and K). Hence, it demonstrates the usefulness of *ilr* transformations for studying plant nutrition. It should be emphasized that the *ilr* method is complementary to studying untransformed nutrient concentrations – it does not always provide further information but rather removes any possible bias of working from untransformed data. In this respect, this study demonstrates that the *ilr* method provides a different perspective for explaining the ecology of RM seedlings. Finally, our study also provides a valuable set of foliar nutrient data for SM and RM seedlings, which are currently sparse in the literature, together with *ilr* balances of SM that were computed from a comprehensive list of studies. More studies should focus on foliar nutrition of tree seedlings as a means of elucidating their potential for establishing and surviving in new environments under climate change.

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# CONCLUSION

Le but général de cette thèse de doctorat a été d'étudier un élément important permettant de mieux prédire la migration de l'ES, soit l'acclimatation nutritive et la régénération de ses semis aux conditions de sol et de couvert aux limites de sa distribution. De ce projet de doctorat ont émergés plusieurs résultats innovants. Dans un premier temps, le Chapitre I a permis de démontrer que les espèces conifériennes ont un effet négatif sur la nutrition foliaire des semis d'ES parce qu'ils réduisent le Ca et Mg foliaire, lesquels sont reconnus comme importants pour leur croissance et survie. Cet effet a été observé indépendamment de la localisation étudiée, et résulte d'une plus forte acidité du sol conditionnée par la présence des conifères. À cela s'ajoute un effet site qui implique que les semis poussant le plus au Nord de la distribution de l'érable à sucre ont également des concentrations nutritives foliaires plus faibles, ce qui peut donc exacerber l'effet négatif de la présence des conifères. Au vu des résultats de ce chapitre et d'autres études de la littérature (e.g. McCarragher et al., 2011), la part du climat dans l'explication de cet effet site apparait comme prépondérant. Cependant, étant donné qu'un seul gradient a été étudié au sein de ce chapitre, d'autres analyses à des latitudes similaires sont nécessaires afin de pouvoir généraliser avec confiance ces résultats sur l'impact du climat. Il serait également intéressant de coupler ces analyses avec des études sous des conditions mieux contrôlées afin de pouvoir isoler spécifiquement les variables d'intérêt. Par exemple, la mise en place d'expériences de croissance en serre à différents niveaux de disponibilité en nutriments et avec des graines d'ES venant des trois localisations étudiées au Chapitre I permettrait de dissocier les parts

d'acclimatation (i.e. à base phénotypique) et d'adaptation (i.e. à base génétique) sur l'évolution de leur nutrition foliaire.

En tenant compte des résultats du Chapitre I, il apparait donc que l'établissement de l'ES au sein de la forêt boréale devrait se faire à une plus faible intensité que celle initialement prédite sur la seule base de l'optimum climatique. D'ailleurs, Boisvert-Marsh et al. (2014) ont récemment estimé que la vitesse actuelle de migration de l'ES est en dessous de celle calculée sur la base d'un maintien de l'optimum climatique en suivant les changements climatiques (0,4 km $an^{-1}$ contre 4,9 km $an^{-1}$, respectivement). Les résultats de cette thèse démontrent donc que les conditions de sols au sein de la forêt boréale sont très probablement une des raisons expliquant ce retard de migration. Cette observation met en valeur l'importance de l'impact des interactions biotiques sur la limite de distribution des espèces végétales, et contribue à diminuer le manque de connaissances que l'on a sur ces processus. En ce sens, elle s'ajoute aux études qui suggèrent que la vitesse de migration des arbres devrait être ralentie par la compétition interspécifique que l'on retrouve au sein du nouvel environnement (Corlett and Westcott, 2013). Les espèces résidentes, en plus d'être mieux adaptées aux conditions locales autres que climatiques, ont également l'avantage numérique. Sur le long terme, une amélioration des conditions de sol au sein de la forêt boréale avec l'augmentation des températures est attendue. Puisque l'ES est une espèce compétitrice considérée comme trans-successionnelle (Nolet et al., 2008), on peut envisager que ce changement lui sera profitable.

D'autre part, les résultats du Chapitre II indiquent que la capacité de régénération de l'ES au sein de forêts de conifères pourrait être également dépendante du type de conifères présents ainsi que des caractéristiques physiques, chimiques et minéralogiques du sol. Par exemple, la probabilité d'établissement de l'ES serait très faible, voire improbable, sur des sites au sol très acide dominés par la pruche ou encore le cèdre. Cependant, dans d'autres cas, la dissolution des minéraux par les champignons ectomycorhiziens des racines serait favorisée en présence de certains

conifères tels que l'épicéa, le sapin ou encore le pin, ce qui peut favoriser la nutrition des semis d'érable à sucre. Cependant, il est à noter que ce mécanisme est hautement dépendant des propriétés du sol, impliquant donc des résultats différents sur des sites possédant des minéralogies et des textures du sol complètement différentes. Des études supplémentaires sur différents types de sol sont donc nécessaires afin de mieux comprendre les mécanismes sous-jacents de ce processus. Ces études pourraient, par exemple, allier des analyses de séquençage ADN pour l'identification de mycorhizes et de bactéries de la rhizosphère, ainsi que l'utilisation de traceurs isotopiques (e.g. $^{87}Sr/^{86}Sr$) pour déterminer l'origine de l'acquisition de nutriments.

Le Chapitre II a également permis de conclure que la présence de FG peut empêcher la régénération des semis d'ES. À St. Hippolyte, ce résultat est principalement la conséquence d'une canopée plus dense qui provoque une plus faible disponibilité de la lumière à un seuil critique pour la survie des semis d'ES. De manière générale, les résultats obtenus rejoignent les conclusions de Hane et al (2003) et permettent d'éclaircir les causes du remplacement progressif de l'ES par le FG. Morin et al. (2008) ont prédit une réduction significative des populations d'ES situés au Sud de la distribution actuelle (25% de réduction de la distribution de l'espèce avec un réchauffement de 3,2°C) en se basant sur les taux spécifiques de migration d'après les études paléoécologiques du dernier cycle de glaciation-déglaciation. Solarik et al. (2016) ont également prédit une diminution de 5 à 30% des taux de germination de l'ES au Sud de sa distribution (sur des scénarios de réchauffement climatique de +2 à +7°C). On peut supposer que le remplacement de l'ES par le FG pourrait exacerber cette contraction. D'après nos résultats et afin de favoriser le maintien de l'ES au sein des érablières à hêtre, un traitement sylvicole combinant la suppression des gaulis de FG avec une récolte de faible intensité des FG matures, tel que proposé par Nolet et al (2015), apparait comme une solution possible.

Afin d'améliorer notre compréhension de la physiologie de la nutrition des semis d'ES sous couvert résineux, une méthode novatrice de diagnostique foliaire qui repose sur les transformations en log-ratios isométriques a été utilisée dans le Chapitre III. Cette technique a permis de confirmer que la présence de conifères entraîne un débalancement nutritif des semis d'ES au travers d'une réduction du Ca et du Mg foliaire. Ce débalancement se fait dans le même sens que celui des arbres matures diagnostiqués en déclin suite à l'appauvrissement en Ca et en Mg dans les sols forestiers par les retombées atmosphériques acides. D'autre part, une comparaison avec les balances nutritives foliaires de l'ER a permis d'identifier que ce dernier est capable de maintenir un équilibre nutritionnel foliaire avec l'augmentation de l'abondance en conifères. Cette observation est le résultat d'une plus grande plasticité nutritionnelle face à des conditions environnementales contrastées, et n'aurait pu être constaté sans l'utilisation novatrice des log-ratios isométriques. La forte exigence nutritive de l'ES est probablement la cause des différences de succès migratoire observées entre ces deux espèces. Les résultats du Chapitre III démontrent l'utilité des transformations en log-ratio isométriques comme méthode complémentaire aux traditionnelles comparaisons de nutriments bruts. Bien que cette méthode ne soit pour l'instant qu'utilisée dans un contexte agronomique ou de production ligneuse, son utilisation routinière en écologie permettrait d'éliminer certains biais potentiels et d'approfondir notre compréhension de l'écophysiologie des plantes.

De manière générale, il est important de retenir que tous les semis dont la nutrition a été étudiée au sein de cette thèse sont des individus qui se sont développés de manière naturelle sur les parcelles échantillonnées. Par conséquent, ces individus étaient ceux les plus robustes et adaptés pour survivre aux conditions environnementales locales. Ce point souligne donc l'importance et l'aspect conservateur de nos résultats qui indiquent un effet négatif de la présence de conifères sur la nutrition foliaire des semis d'ES. Le fait d'avoir utilisé des expérimentations en

milieu naturel a permis d'observer la réponse attendue des semis aux changements de végétation dominante et de conditions de sol. Cependant, la conséquence de ce type d'expérimentation est qu'il est bien souvent difficile de séparer et quantifier l'impact des différents facteurs environnementaux ainsi que leurs interactions. De plus, étant donné qu'il est impossible de mesurer toutes les variables présentes, cela complique fortement la mise en place d'inférences robustes sur les facteurs d'intérêt. Bien que les conclusions de cette thèse reposent sur des résultats solides, l'utilisation d'expérimentations contrôlées ciblés sur un ou deux facteurs spécifiques permettrait de les généraliser. D'autre part, des études complémentaires portant sur la mycorhization de l'ES au sein de la forêt boréale permettraient d'approfondir les travaux de cette thèse sur son acclimatation nutritive. Le développement d'endomycorhizes arbusculaires associées à l'ES permettrait d'améliorer sa nutrition sur les sols acides en réduisant l'absorption toxique de l'Al (Ouimet et al., 1996). Cependant, leur développement est sensible au pH du sol et à l'appauvrissement en Ca dans les tissus de la plante (Jarstfer et al., 1998). En dessous d'un pH de 5, les endomycorhizes arbusculaires sont progressivement remplacées par les ectomycorhizes (lesquelles dominent au sein des forêts boréales et forment des associations avec les espèces résineuses) du fait de leurs optimums écologiques respectifs (Read, 1991). Il n'est donc pas exclu que des différences d'intensité de mycorhization soient responsables d'une certaine part de variation dans la qualité de la nutrition des semis étudiés au sein de cette thèse. Également, dans un cadre ciblant spécifiquement l'impact du réchauffement climatique, des analyses complémentaires portant sur le statut hydrique des semis d'ES permettraient de finaliser notre compréhension de leur acclimatation nutritive. Cela permettrait aussi de confirmer une des hypothèses résultantes du Chapitre II, i.e. la litière des conifères affecterait négativement la régénération et la croissance des semis d'ES au travers d'une diminution de l'humidité du sol. Cette hypothèse pourrait être testée en milieu naturel ou contrôlé via l'analyse des isotopes stables du carbone (Schifman et al. 2011).

Spécifiquement, cette méthode utilise la discrimination du $^{13}C$ sur le $^{12}C$ dans les tissus de la plante afin d'obtenir un indicateur sensible et à long terme du statut hydrique de celle-ci, le $^{13}C$ étant retrouvé en plus grande proportion chez les plantes subissant un stress hydrique. Enfin, il reste à mentionner un dernier facteur à approfondir concernant la compréhension de la régénération des semis d'ES, celui de l'impact de l'herbivorie et des pathogènes. Au sein du Chapitre II, les résultats soulignent l'importance de la considération d'une herbivorie préférentielle des semis d'ES pour leur survie au sein des érablières à hêtre. Ces dommages foliaires ont été attribués aux insectes. Cependant, même si aucun dommage lié aux plus grands herbivores (e.g. chevreuil, lièvre) n'ait été observé, leur importance a été démontrée dans d'autres études (e.g. Long et al. 2007). Un dispositif spécialement conçu pour étudier l'impact de l'herbivorie sur la survie des semis d'ES et qui séparerait l'impact de ces deux communautés d'herbivores s'avèrerait particulièrement utile. En outre, les semis des parcelles dominées par les conifères sont ceux qui ont subi le moins de dommages foliaires liés à la pression des herbivores. Urli et al. (2016) ont d'ailleurs récemment observés que des semis d'ES transplantés au-delà de leur distribution naturelle bénéficiaient d'une libération de la pression des insectes et herbivores. Cet effet de libération des ennemis naturels tel qu'annoncé par l'hypothèse de Janzen-Connell (Janzen, 1970 ; Connell, 1971) serait potentiellement le même avec les pathogènes fongiques (Brown and Vellend, 2014), lesquels sont également responsables de fortes mortalités au sein de la distribution de l'ES (Cleavitt et al., 2011 ; 2014). De plus amples études sont donc nécessaires afin de pouvoir évaluer l'aspect bénéfique de cet effet dans un contexte de migration sous les changements climatiques.

En perspective, les résultats de cette thèse, et particulièrement la caractérisation approfondie des variables du sol conjointement avec les nutriments foliaires d'ES, pourront servir d'outils à intégrer en modélisation pour déterminer si l'amplitude écologique de l'ES va bouger, s'étendre ou au contraire se réduire. Un

des exemples serait de les utiliser pour calibrer le modèle biogéochimique SAFE (Bélanger et al., 2002; Thiffault et al., 2007). Ce dernier peut simuler à long terme la composition chimique du sol (ex. pH, cations échangeables, saturation en base) et sa solution (ratio Ca:Al, etc.). En faisant varier la composition du couvert ainsi que la température et la teneur en eau du sol selon les projections d'Ouranos pour influencer les sources/puits d'ions et les réactions chimiques du sol, il serait possible de déterminer les risques pour l'ES d'être exposé à des conditions de sol qui pourraient s'avérer désavantageuses pour sa santé nutritionnelle et sa vigueur en général. Ce genre d'information permettrait d'aider les ingénieurs forestiers à établir des stratégies idéales de gestion pour cette essence. D'après les résultats de cette thèse, et si les enjeux socio-économiques vont en la faveur de conserver une étendue de distribution de l'ES similaire à celle actuelle, certaines mesures peuvent être envisagées. Par exemple, une expansion assistée de sa distribution (« assisted range expansion » ; (Ste-Marie et al., 2011) peut être effectuée juste après sa limite de distribution, au sein de la forêt boréale, en alternant coupes partielles et établissement de l'ES sur des sites aux sols considérés comme les plus propices. Cela permettrait une transition plus rapide de l'état de forêt boréale vers un état de forêt mixte, mimant ainsi au mieux l'expansion naturelle de la distribution de l'ES. L'utilisation de chaulage afin d'augmenter la disponibilité en cations basiques peut également être envisagée afin d'améliorer la compétitivité de l'ES dans les zones de transition où les sols seraient pauvres en éléments nutritifs. Cependant, ce type de traitement doit être envisagé au cas par cas en raison des potentiels risques écologiques (Moore et al., 2015). Dans un autre contexte, une suppression des gaulis de FG avec une récolte de faible intensité des FG matures, tel que cité précédemment, permettrait de limiter le remplacement de l'ES par le FG au sein des peuplements à forte valeur socio-économique.

Bien que cette thèse ait portée exclusivement sur l'ES, les processus mis en valeur au sein de celle-ci soulignent l'importance des interactions biotiques comme facteurs influençant la limite de distribution des espèces végétales en général. En raison de la complexité liée à leur étude, encore peu de travaux portent sur ce type d'interactions dans un contexte de changements climatiques, les rendant difficiles à prédire et à intégrer dans les modèles. D'un point de vue de la nutrition des plantes, une des problématiques majeures de la prochaine décennie est probablement l'étude des effets rétroactifs entre les plantes et le sol (« plant-soil feedbacks ») sur le long terme avec le réchauffement climatique. Ces effets rétroactifs agissent comme des filtres de sélection des communautés végétales. Cependant il y a actuellement peu d'informations sur les conséquences rétroactives d'un changement des propriétés du sol (e.g. décomposition de la litière, humidité du sol, cycle des nutriments) par une augmentation de température ou l'action d'une espèce migrante (van der Putten et al., 2016). La question est de pouvoir les généraliser et surtout de savoir quand ces changements d'effets interviennent. De même, tandis que l'emphase actuelle est placée sur les interactions biotiques négatives limitant la migration des espèces, il reste encore plus d'interrogations sur les interactions positives telles que la complémentarité, la facilitation ou encore le mutualisme (Afkhami et al., 2014). D'autre part, une autre problématique majeure est la considération de la plasticité phénotypique, et ses tenants génétiques, comme adaptation des espèces aux conditions changeantes de l'environnement (Christmas et al., 2016). Les techniques d'analyse du génome et du transcriptome sont de plus en plus communément utilisées et permettraient d'investiguer l'adaptation des espèces et les mécanismes génétiques sous-jacents à l'adaptation et la plasticité le long de gradients environnementaux. Enfin, un des grands défis pour la recherche sur la nutrition foliaire reste la mise en place de normes nutritionnelles aux différents stades de vie des plantes ainsi qu'une généralisation de l'utilisation de diagnostiques robustes. De nos jours, de nombreuses études sont encore basées sur l'utilisation d'indices obsolètes ou de diagnostiques foliaires dont les biais sont reconnus.

# APPENDICE A

Percentage contribution of each species present within each study site as a function of forest type (H: hardwood stands, Mx: mixed hardwood-conifer stands, C: conifer-dominated stands).

| Species | Lac Labelle | | | St Hippolyte | | | Windsor | | |
|---|---|---|---|---|---|---|---|---|---|
| | H | Mx | C | H | Mx | C | H | Mx | C |
| *Acer saccharum* | 32.5 | 12.5 | 0 | 77.75 | 19.75 | 0 | 72.5 | 50.5 | 6.75 |
| *Acer rubrum* | 30 | 27.5 | 7.5 | 0 | 14.75 | 10 | 0 | 0 | 1.75 |
| *Betula papyfera* | 22.5 | 22.5 | 12.5 | 2.25 | 40 | 36.5 | 0 | 0 | 0 |
| *Betula alleghaniensis* | 0 | 0 | 0 | 12 | 0 | 0 | 7.5 | 17.5 | 20 |
| *Tilia americana* | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 12 | 0 |
| *Fagus grandifolia* | 0 | 0 | 0 | 5.75 | 2.5 | 1.25 | 0 | 3.75 | 1.75 |
| *Populus grandidentata* | 0 | 0 | 0 | 0 | 13.5 | 0 | 0 | 0 | 0 |
| *Abis balsamea* | 15 | 32.5 | 42.5 | 2.25 | 9.5 | 28.5 | 0 | 1.25 | 8.25 |
| *Pinus strobus* | 0 | 0 | 0 | 0 | 0 | 5.75 | 0 | 0 | 0 |
| *Picea sp* | 0 | 0 | 0 | 0 | 0 | 11.75 | 0 | 0 | 0 |
| *Thuja occidentalis* | 0 | 5 | 37.5 | 0 | 0 | 6.25 | 0 | 0 | 6.75 |
| *Tsuga canadensis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 53.5 |
| Hardwoods | 85 | 62.5 | 20 | 97.75 | 90.5 | 47.75 | 100 | 83.75 | 30.25 |
| Conifers | 15 | 37.5 | 80 | 2.25 | 9.5 | 52.25 | 0 | 16.25 | 68.5 |

APPENDICE B

Mehlich III extractable levels of cations and $P\text{-}PO_4^{3-}$ within each study site as a function of forest type (H: hardwood stands, Mx: mixed hardwood-conifer stands, C: conifer-dominated stands). Pearson correlation coefficients between values of respective nutrients (Ca, Mg, K and P) or Al as determined by the Mehlich III extraction (forest floor) and PRS probes (just below the forest floor) are presented.

| | | FH horizon | | | | |
|---|---|---|---|---|---|---|
| Site | Cover | P | K | Ca | Mg | Al |
| | | µg / g | | | | |
| Lac Labelle | - | 242 ± 26 | 626 ± 53 | 1668 ± 139 | 176 ± 12 | 493 ± 78 |
| St. Hippolyte | - | 78.2 ± 13.6 | 461 ± 30 | 2847 ± 255 | 200 ± 13 | 1137 ± 191 |
| Windsor | - | 106 ± 17 | 246 ± 29 | 1821 ± 549 | 229 ± 70 | 1545 ± 226 |
| Lac Labelle | H | 316 ± 52 | 687 ± 88 | 1859 ± 274 | 200 ± 28 | 340 ± 30 |
| | Mx | 215 ± 40 | 637 ± 139 | 1383 ± 287 | 158 ± 20 | 697 ± 201 |
| | C | 196 ± 19 | 554 ± 41 | 1761 ± 117 | 170 ± 9 | 441 ± 59 |
| St. Hippolyte | H | 90.4 ± 38.0 | 423 ± 32 | 2366 ± 361 | 181 ± 31 | 1812 ± 377 |
| | Mx | 78.6 ± 18.2 | 509 ± 64 | 3255 ± 587 | 230 ± 12 | 768 ± 104 |
| | C | 65.6 ± 12.6 | 451 ± 59 | 2920 ± 330 | 189 ± 16 | 831 ± 151 |
| Windsor | H | 97.4 ± 30.3 | 257 ± 12 | 1482 ± 47 | 172 ± 18 | 1856 ± 392 |
| | Mx | 155 ± 29 | 327 ± 65 | 3086 ± 1568 | 411 ± 190 | 1412 ± 539 |
| | C | 65.3 ± 9.8 | 153 ± 15 | 897 ± 36 | 104 ± 7 | 1368 ± 266 |
| Correlation with PRS probes | | **0.38 *** | **0.59 ***** | **0.58 ***** | **0.36 *** | **0.87 ***** |

| Site | Cover | B horizon | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | P | | K | | Ca | | Mg | | Al | |
| | | μg / g | | | | | | | | | |
| Lac Labelle | - | 5.38 | ± 1.89 | 12.0 | ± 2.1 | 56.2 | ± 11.4 | 9.85 | ± 0.55 | 1810 | ± 56 |
| St. Hippolyte | - | 0.92 | ± 0.19 | 41.0 | ± 3.8 | 123 | ± 25 | 11.0 | ± 1.7 | 1961 | ± 38 |
| Windsor | - | 13.0 | ± 6.6 | 23.4 | ± 5.7 | 485 | ± 389 | 54.4 | ± 39.3 | 1709 | ± 149 |
| Lac Labelle | H | 10.2 | ± 5.2 | 11.6 | ± 4.1 | 79.0 | ± 33.4 | 9.88 | ± 0.80 | 1986 | ± 76 |
| | Mx | 3.54 | ± 0.47 | 14.8 | ± 4.5 | 46.1 | ± 3.5 | 10.5 | ± 0.8 | 1741 | ± 69 |
| | C | 2.46 | ± 0.38 | 9.43 | ± 2.8 | 43.6 | ± 6.4 | 9.18 | ± 1.35 | 1704 | ± 96 |
| St. Hippolyte | H | 1.39 | ± 0.50 | 47.9 | ± 6.7 | 135 | ± 33 | 11.5 | ± 1.5 | 1893 | ± 56 |
| | Mx | 0.80 | ± 0.11 | 37.9 | ± 6.0 | 166 | ± 62 | 13.8 | ± 4.5 | 1955 | ± 77 |
| | C | 0.58 | ± 0.07 | 37.2 | ± 7.4 | 69.2 | ± 16.6 | 7.68 | ± 0.72 | 2034 | ± 59 |
| Windsor | H | 5.20 | ± 2.09 | 36.4 | ± 9.9 | 165 | ± 46 | 23.2 | ± 4.9 | 1656 | ± 251 |
| | Mx | 27.5 | ± 19.0 | 13.8 | ± 7.1 | 1230 | ± 1176 | 128 | ± 119 | 1594 | ± 346 |
| | C | 6.18 | ± 3.67 | 19.9 | ± 10.7 | 61.0 | ± 17.1 | 11.7 | ± 0.7 | 1877 | ± 215 |

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